The Role of Fine-Scale Habitat Associations in Structuring Spider Assemblages: Determinants of Spatial Patterns In Community Composition

Stephanie M. Cobbold

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Stephanie M. Cobbold
Utah State University

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THE ROLE OF FINE-SCALE HABITAT ASSOCIATIONS IN STRUCTURING SPIDER ASSEMBLAGES: DETERMINANTS OF SPATIAL PATTERNS IN COMMUNITY COMPOSITION

by

Stephanie M. Cobbold

A dissertation submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Ecology

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UTAH STATE UNIVERSITY
Logan, Utah
2012
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ABSTRACT

The Role of Fine-scale Habitat Associations in Structuring Spider Assemblages:
Determinants of Spatial Patterns in Community Composition

by

Stephanie M. Cobbold, Doctor of Philosophy
Utah State University, 2012

Major professor: James A. MacMahon
Department: Biology

Elucidating the ecological determinants of community structure and how they vary spatially has a long history in ecology, but there still is no consensus on the mechanisms behind diversity patterns. The primary objective of this dissertation was to focus on spider assemblages to investigate how the fine-scale habitat associations of organisms may drive their community composition at larger scales. Research was conducted in the Bear River Mountains, Utah, in an attempt to elucidate the potential role of species-microhabitat associations in driving three well-known patterns of community composition that have typically been investigated at broad scales: 1) elevation gradients of species diversity, 2) the response of species assemblages to neighboring habitat structure and 3) community composition at the edges of habitat patches.

Slope aspect was a significant predictor of spider density and species richness when communities were compared at the same elevation, suggesting that fine-scale topographic variables may play an important role in shaping elevational patterns of
species composition. Cursorial spider composition was strongly linked to site temperature only, whereas differences across web spider assemblages significantly increased with dissimilarities in woody plant cover and temperature.

The study on the effects of neighboring habitat structure revealed markedly reduced cursorial spider densities in shrubs without surrounding structure, and more cursorial species in control shrubs, whereas web spiders lacked any significant response to treatments. These contrasting responses indicate that data should be collected at larger spatial extents for mobile species, and that mobility may mediate the outcome of surrounding habitat modifications on the local composition of communities.

In the last study, I focused on communities in which the edge-dwelling spiders *Theridion* and *Dictyna* strongly differed in terms of concealment and substrate generalization and found that microhabitat choice may affect the sensitivity of species to habitat geometry, a characteristic associated with habitat fragmentation.

This work suggests that a better understanding of the links between the biological traits of species and their fine-scale environmental requirements may help uncover the mechanisms behind spatial patterns of community composition at larger scales.
Ecologists strive to identify the mechanisms that drive the identity and abundance of species in different locations, because a better understanding of such factors enables them to better predict the effects of habitat modification on organisms, and to identify landscapes in which species are likely to benefit from conservation interventions. However, there is still no consensus on the mechanisms behind geographical variation in species diversity. The primary objective of this dissertation was to focus on spider assemblages to investigate how the fine-scale habitat associations of organisms may drive the composition of their communities at larger scales. Research was conducted in the Bear River Mountains, Utah, in an attempt to elucidate the potential role of species-microhabitat associations in driving three well-known patterns of community composition that have been typically investigated at broad scales: 1) elevation gradients of species diversity, 2) the response of species assemblages to neighboring habitat structure and 3) community composition at the edges of habitat patches.

I found that fine-scale topographic variables related to slope aspect may play an important role in shaping elevational patterns of species composition. In addition, two species characteristics that may be useful predictors of sensitivity to habitat modification
at larger scales were identified: mobility and habitat preference. This work suggests that a better understanding of the links between the biological traits of species and their fine-scale environmental requirements may help uncover the mechanisms behind spatial patterns of community composition at larger scales.
This thesis is dedicated to my parents, Nelly and Peter Cobbold, for their love and endless support
The Spider’s Web, lithograph by the Reverend Richard Cobbold, my great-great-great uncle (Ipswich, 1797 - Wortham, Suffolk, 1877).
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I thank all the members of my family for their support, especially my parents and brother, who are the most loving and encouraging people I have ever known. Finally, I thank my best friend and husband, Ryan O’Donnell, for his unconditional love and understanding. We have spent many wonderful times, and I look forward to the new adventures that await us.

Stephanie M. Cobbold
# CONTENTS

<table>
<thead>
<tr>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT ....................................................................................................................... iii</td>
</tr>
<tr>
<td>PUBLIC ABSTRACT ......................................................................................................... v</td>
</tr>
<tr>
<td>ACKNOWLEDGMENTS ......................................................................................................... ix</td>
</tr>
<tr>
<td>LIST OF TABLES ........................................................................................................... xiii</td>
</tr>
<tr>
<td>LIST OF FIGURES ......................................................................................................... xiv</td>
</tr>
</tbody>
</table>

## CHAPTER

1. INTRODUCTION .................................................................1

   References .................................................................................................................5

2. FINE-SCALE TOPOGRAPHY SHAPES SPIDER COMMUNITY STRUCTURE ALONG AN ELEVATIONAL GRADIENT: LINKS BETWEEN GUILD IDENTITY, TEMPERATURE, AND HABITAT STRUCTURE ......................................................11

   Abstract ..................................................................................................................11
   Introduction .............................................................................................................12
   Materials and Methods ..........................................................................................15
   Results ......................................................................................................................19
   Discussion ................................................................................................................23
   References ................................................................................................................28

3. GUILD MOBILITY PREDICTS SPIDER DIVERSITY: LINKS BETWEEN FORAGING BEHAVIOR AND SENSITIVITY TO ADJACENT VEGETATION STRUCTURE ..............................................................41

   Abstract ..................................................................................................................41
   Introduction .............................................................................................................42
   Materials and Methods ..........................................................................................44
   Results ......................................................................................................................49
   Discussion ................................................................................................................51
   References ................................................................................................................55
4. PATCH SHAPE ALTERS SPIDER COMMUNITY STRUCTURE: LINKS BETWEEN MICROHABITAT CHOICE AND SENSITIVITY TO INCREASED EDGE HABITAT .........................................................64

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>64</td>
</tr>
<tr>
<td>Introduction</td>
<td>65</td>
</tr>
<tr>
<td>Materials and Methods</td>
<td>68</td>
</tr>
<tr>
<td>Results</td>
<td>72</td>
</tr>
<tr>
<td>Discussion</td>
<td>74</td>
</tr>
<tr>
<td>References</td>
<td>80</td>
</tr>
</tbody>
</table>

CONCLUSION ........................................................................................................92

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>References</td>
<td>92</td>
</tr>
</tbody>
</table>

APPENDIX ........................................................................................................97

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>CURRICULUM VITAE</td>
<td>103</td>
</tr>
<tr>
<td>Table</td>
<td>Description</td>
</tr>
<tr>
<td>---------</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>2.1</td>
<td>ANOSIM results for comparisons of spider community structure on all aspects at a given elevation (global analysis) and on the two slope aspects that contained the most different spider assemblages at each elevation</td>
</tr>
<tr>
<td>2.2</td>
<td>The percentage contribution of individual genera to pairwise dissimilarities between the two aspects that contained the most different spider assemblages at each elevation, based on the Bray-Curtis similarity index (SIMPER)</td>
</tr>
<tr>
<td>2.3</td>
<td>Average temperature, minimum and maximum temperature, and percent cover of woody plants and forbs at each site</td>
</tr>
<tr>
<td>2.4</td>
<td>Results of multiple regressions on distance matrices using a permutation method with the squared matrix of pairwise dissimilarity in spider genus composition (dependent matrix) and pairwise geographical and environmental distances between sites (independent matrices)</td>
</tr>
<tr>
<td>3.1</td>
<td>The percentage contribution of individual genera to pairwise dissimilarities between the control, addition and removal treatments based on Bray-Curtis similarity indices (SIMPER)</td>
</tr>
<tr>
<td>4.1</td>
<td>Location and number of <em>Theridion</em> and <em>Dictyna</em> webs within cubic (<em>C</em>) and elongated (<em>E</em>) modules over the two combined observation periods</td>
</tr>
<tr>
<td>A.1</td>
<td>List of spiders collected in big sagebrush shrubs in Logan Canyon, Utah</td>
</tr>
</tbody>
</table>
LIST OF FIGURES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Range (in degrees) of each slope aspect in this study</td>
<td>38</td>
</tr>
<tr>
<td>2.2</td>
<td>Mean spider abundance per 0.1 m³ (volume representative of shrub size at our field sites) at each sampling location</td>
<td>39</td>
</tr>
<tr>
<td>2.3</td>
<td>Mean spider species richness per 0.1 m³ (volume representative of shrub size at our field sites) at each sampling location</td>
<td>40</td>
</tr>
<tr>
<td>3.1</td>
<td>Definition of shrub understory in this study</td>
<td>61</td>
</tr>
<tr>
<td>3.2</td>
<td>The three experimental treatments of the shrub understory</td>
<td>62</td>
</tr>
<tr>
<td>3.3</td>
<td>Mean cursorial and web spider density (A) and species richness (B) per 0.1 m³ (volume representative of shrub size at our field site) in the three understory treatments</td>
<td>63</td>
</tr>
<tr>
<td>4.1</td>
<td>Difference in the amount of patch edge intercepted by a hypothetical isoline of visual discrimination acuity (circle) of a visual arthropod (black dot) in a square compared to a rectangle of identical surface area</td>
<td>88</td>
</tr>
<tr>
<td>4.2</td>
<td>Cubic and elongated modules</td>
<td>89</td>
</tr>
<tr>
<td>4.3</td>
<td>Differences in concealment in <em>Theridion</em> and <em>Dictyna</em></td>
<td>90</td>
</tr>
<tr>
<td>4.4</td>
<td>Family-level box plots of total spider abundance on cubic modules and elongated modules</td>
<td>91</td>
</tr>
</tbody>
</table>
CHAPTER 1
INTRODUCTION

Elucidating the ecological determinants of community structure and how they vary spatially has a long history in ecology (reviewed in Parmesan et al. 2005). Models that predict species distributions and abundance are widely used in ecology and biogeography to investigate the determinants of species geographic ranges (Parmesan et al. 2005), to predict the effects of habitat modifications on the conservation of biodiversity and to identify landscapes in which species are likely to benefit from conservation interventions (Illan et al. 2010). However, while diversity patterns are increasingly well documented and understood, the variables that drive them remain a significant intellectual challenge (Gaston 2000), and multiple mechanisms have been suggested to explain geographical variation in species richness (Gaston 2000; Evans et al. 2005; Rahbek 2005; Sanders et al. 2007).

The factors that shape community structure are difficult to understand, because of the confounding influence of multiple factors including evolutionary history (Ricklefs and Schluter 1993), variation in the composition of regional species pools (Cornell 1999) and collinearity among explanatory variables. In addition, taxonomic diversity gradients occur at many spatial scales, ranging from a few meters (e.g. Norris et al. 2002) to thousands of kilometers, as in the latitudinal diversity gradient (Hillebrand 2004). The nature and relative influence of the drivers of diversity may differ with scale (Field et al. 2009), and it has become increasingly apparent that the development of mechanistic theories of diversity patterns will be enhanced as we learn more about the nature and roles of processes at different spatial grains and extents (Gaston 2000).
Since different species respond to their environment at different spatial and temporal scales (Wiens and Milne 1989), knowledge of the pertinent scale at which species interact with the landscape should provide important guidelines for the design of studies of the determinants of community structure. While many terrestrial organisms experience their environment at relatively small scales (millimeters to meters), studies tend to analyze data at resolutions that are greater than the home ranges of the species under investigation (Suggitt et al. 2011) even though the importance of local factors has been recognized for some time. As a result, these investigations may be missing valuable information on the mechanisms that drive community composition. For instance, local habitat characteristics may have a stronger effect on the distribution of organisms that are small-bodied (Farji-Brener et al. 2004) or that have limited movement capacity (Suarez-Seoane and Baudry 2002), because they perceive the landscape in more detail and therefore respond to finer-scale heterogeneity.

An additional challenge with broad-scale studies is that the spatial and temporal scales they consider are sufficiently extensive that a mechanistic understanding of cause-effect relationships is difficult to gain, especially through experimentation. Small-scale experiments, on the other hand, allow for replication in a more controlled environment. Such experiments stimulate theory development, which in turn stimulates replication in other systems at increasingly larger scales (Benton et al. 2007). Small-scale systems have historically been successful in providing information on ecological processes that are applicable at larger scales (e.g., Robinson and Edgemon 1989; Bonsall and Hassell 1997; Benton and Beckerman 2005), and have even provided insights for global issues, such as the effect of climate change on species distributions (Davis et al. 1998).
Spider communities are suitable systems to study the effect of fine-scale habitat associations as drivers of community composition at bigger scales because spiders are abundant, widespread, and diverse (Wise 1993; Hatley and MacMahon 1980), and are very sensitive to fine-scale habitat characteristics and microclimatic conditions (Wise 1993; Sattler et al. 2010). For instance, several studies describe distinctive thermal tolerances and preferences across species (Riechert and Tracy 1975; Lubine et al. 1993; Li and Jackson 1996; Schmalhofer 1999), and demonstrate that different species select for specific habitat structures (Abraham 1983; Marc and Canard 1997; Heikkinen and MacMahon 2004). In addition, spiders provide good cases to investigate how differences in biological traits may affect the habitat associations of species because spiders can be classified into two ecologically distinct guilds based on their foraging behavior: sedentary spiders that build webs and are restricted to specific hunting sites, and cursorial species which do not build webs and actively pursue their prey (Wise 1993).

The aim of this dissertation is to build on large-scale studies of patterns of community composition, by examining the determinants of community composition at finer spatial extents. Specifically, I investigate how an understanding of species-microhabitat associations may provide important clues on the mechanisms behind community patterns at broader scales. In Chapter 2, I examine the possibility that inconsistent findings on the factors that shape elevational patterns of species diversity may be due to the omission of fine-scale information on species-environment interactions. At the regional scale, elevation gradients translate into gradual changes in ambient temperature, radiation, cloud cover, precipitation, and wind speed (Bonan 2002; Geiger 1950). However, at smaller scales, variation in topography (slope, aspect), soils
and land cover create a mosaic of microclimates that differ from the prevailing macroclimate (Bonan 2002). Characteristics of local topography such as slope aspect are typically overlooked in elevational studies (e.g. Olson 1994; Muster 2002). Yet, differences in insolation on different slope aspects generate differences in microclimate (temperature and moisture regimes) and vegetation characteristics (species composition, density, and structure) (Brunn et al. 2006; Desta et al. 2004) that may affect the overall elevational pattern of species diversity. I assess whether the composition of spider communities can significantly differ across different slope aspects at the same elevation, and whether the environmental factors that play a key role in determining community structure may differ among web spiders and cursorial spiders.

In Chapters 3 and 4, I investigate the potential for field experiments to reveal how species differ in their perception of the environment, and how these findings can generate useful and perhaps necessary insights for the design and interpretation of studies of community composition at larger scales. Chapter 3 describes a field experiment that focuses on the possible role of mobility as a predictor of sensitivity to adjacent habitat structure. The effect of landscape heterogeneity on species composition may be particularly important for mobile organisms because they are likely to respond to features on a larger scale than less mobile species (Holland et al. 2005). However, studies of this hypothesis typically consist in quantifying patterns in already-existing landscapes (e.g. Weibull and Ostman 2003; Dauber et al. 2005; Cole et al. 2010), whereas manipulative experiments, which would be subject to fewer confounding variables, are lacking mostly due to the difficulty of conducting experiments at large spatial scales. Since habitat structure and its effects may also operate at smaller scales, especially for small organisms
including spiders (Wing 1984), I studied spider communities inhabiting sagebrush shrubs (Artemisia tridentata) surrounded by modified habitat structures to examine whether the community composition of cursorial species was more strongly affected than that of web-building species.

In Chapter 4, I assess the potential for microhabitat associations to explain patterns of community structure in habitat patches that differ in the amount of edge habitat. Increased habitat edge, one of the most important consequences of habitat fragmentation, negatively affects many organisms in terms of foraging, movement and survival (Burkey 1993; Ostman et al. 2009). While habitat modification and its effects are often documented at spatial scales that span meters to kilometers (e.g. Ewers and Didham 2007), other studies demonstrate that small scale architectural changes in individual plants and artificial structures modify the composition of the spider communities within (Hatley and MacMahon 1980; Heikkinen and MacMahon 2004). A good understanding of these small-scale attributes should improve habitat management plans, because these traits shape the physical architecture of common and invasive plants, thereby affecting the composition of species communities at larger spatial extents (e.g. Pearson 2009). In a field study that focused on two web spider genera that strongly differ in terms of concealment and substrate use, I used artificial shrub modules of identical volume but of different shape to investigate the role of biological attributes in driving edge sensitivity.

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CHAPTER 2

FINE-SCALE TOPOGRAPHY SHAPES SPIDER COMMUNITY STRUCTURE ALONG AN ELEVATIONAL GRADIENT: LINKS BETWEEN GUILD IDENTITY, TEMPERATURE, AND HABITAT STRUCTURE

Abstract

Elevational patterns of diversity are well documented, but the factors that shape them are poorly understood. Inconsistent findings across studies may result from the omission of fine-scale habitat information and from the pooling of species that interact in different ways with their environment. Spiders provide good cases to evaluate these ideas because they are small, microhabitat-sensitive organisms that can be classified into two ecologically different guilds: sedentary spiders that build webs and cursorial species that actively pursue their prey. We tested the hypothesis that the composition of spider communities across different slope aspects significantly differed at a given elevation. We also investigated whether differences in genus composition were shaped by different processes in each guild, by estimating the relative importance of geographic distance, habitat structure and temperature on the community composition of cursorial and web spiders. Elevation and slope aspect were significant predictors of spider density and species richness, and environmental factors played a key role in determining spider community structure. Differences in cursorial spider composition were strongly driven by temperature dissimilarity only, whereas differences across web spider assemblages significantly increased with dissimilarities in woody plant cover and temperature. This

1 This chapter is co-authored by Stephanie M. Cobbold and James A. MacMahon
work suggests that fine-scale topographic variables cannot be ignored, and that a better understanding of the links between the biological traits of species and their environmental requirements should help uncover the mechanisms behind topographic patterns of diversity.

Introduction

Our understanding of the nature and relative importance of the mechanisms that affect the size and diversity of populations along gradients is important not only to correctly understand the ecology of organisms, but also to achieve effective management plans in modified habitats, including the design of conservation and biological control plans. Montane systems in particular are ideal to study geographic variation in the determinants of community structure, because the abiotic environment often varies in predictable ways along elevation gradients (Körner 2007). However, while species distribution patterns with elevation are broadly documented in both plants and animals, the nature of the pattern of diversity is still controversial (McCoy 1990), making it difficult to predict how community composition varies with changes in elevation. Species richness may peak at the highest, lowest, or middle elevation or display no trend, depending on the community and location (Hodkinson 2005; McCoy 1990). In addition, the mechanisms that determine these diversity patterns remain poorly understood (Lessard et al. 2011), and multiple hypotheses have been suggested (Gaston 2000; Evans et al. 2005; Rahbek 2005; Sanders et al. 2007).

Findings may be inconsistent across studies because sampling designs tend to underestimate how organisms differ in their perception of the environment. First, studies
often investigate the trends of grouped species despite the possibility that some may
differ considerably in terms of behavior, life history and environmental requirements
(Krasnov et al. 2010). Second, it is commonly believed that climatic variables are the
large-scale determinants of species distributions, and that land cover, species interactions
and colonization-extinction dynamics become increasingly important at finer scales (Illan
et al. 2010). Yet, the complex topography of mountain habitats offers a wide range of
elevations, slopes and aspects that cause climatic conditions to vary markedly over short
distances, creating a mosaic of different habitat patches with their own microclimate and
vegetation structure (Hodkinson 2005). Since studies typically interpret data at a much
greater resolution than that of the home ranges of the species studied (Suggitt et al. 2011),
it seems reasonable to postulate that we may be missing valuable information on the
mechanisms behind community composition at different elevations. For instance, studies
that sample on a particular slope at a given elevation may reflect more on which species
are able to exploit that specific habitat type rather than the total species diversity present
at that elevation.

Local topography may have a stronger effect on the distribution of small-bodied
organisms, because they respond to finer-scale heterogeneity in the environment than
large-bodied ones (Farji-Brener et al. 2004). Spiders in particular are very sensitive to
fine-scale habitat structure and microclimatic conditions (Wise 1993; Sattler et al. 2010),
but studies of their diversity along elevational gradients typically omit fine-scale,
topographically explicit environmental data, such as the temperature and vegetation
structure of different slope aspects at a same elevation. In addition, the extent to which
these variables contribute to shaping communities, and whether they differ across species
is not well understood. Spider species provide good cases for measuring the relative importance of biological traits on geographic patterns of diversity, because they can be classified into two ecologically different guilds: sedentary spiders that use silk traps to catch their prey and hunters that actively pursue prey (Wise 1993). As a consequence of their particular foraging strategy, different guilds predominate in different habitat structures (Abraham 1983; Heikkinen and MacMahon 2004). Diurnal cursorial species tend to be less localized and may be found wandering in diverse locations, whereas web-builders colonize specific substrates according to the demands of the type of web that they build (Marc and Canard 1997; Abraham 1983).

Here, we assess 12 spider communities inhabiting sagebrush shrubs (Artemisia tridentata) on different slope aspects and elevations in the Bear River Mountains, Utah, USA, to determine whether 1) spider abundance, species richness and community composition significantly differ on different slope aspects at the same elevation and 2) the role of temperature, vegetation structure and geographic location in driving spatial variation in community structure differs among spider guilds. Since spiders are ectotherms, we predicted that temperature should be a strong predictor of community composition in both guilds. However, the guild differences described above led us to expect that topographic differences in habitat structure should be stronger predictors of community composition in web spiders compared to cursorial spiders along elevation gradients.
Materials and methods

Experimental design

We conducted this study on mountain slopes dominated by montane sagebrush steppe along Logan Canyon in the Bear River Mountains, Cache Co., Utah, USA. Big sagebrush (*Artemisia tridentata*) covered more than 25% of the landscape at all sites. At each of three elevations (1715 m, 1915 m, 2345 m), we selected four sites of different slope aspect, each defined by a fixed range of 20 degrees (Fig. 2.1) to reduce overlap between aspects (north (N): 20°-40°, east (E):110°-130°, south (S):200°-220°, and west (W): 290°-310°). Ranges were chosen to maximize differences between aspects, considering that the extremes in temperature are located on slopes that face south-west and north-east (Geiger 1950). On average, sites at a given elevation were located 500 m from each other. At each site, we randomly selected 20 sagebrush shrubs following criteria of size, shape and isolation (Ehmann and MacMahon 1996), and ensured shrubs were within 5 m of the appropriate elevations. Shrubs were at least 6 m apart, with canopies that ranged between 40 cm and 100 cm in any one dimension, to standardize the amount of substrate available to spiders and the likelihood of aerial colonization (Hatley and MacMahon 1980). The selection of only one shrub species (big sagebrush) for spider collection, in stands in which it dominated, enabled us to reduce habitat differences other than climate. For each shrub, we measured canopy height, width, and length to estimate canopy volume following the formula for the volume of an ellipsoid (Hatley and MacMahon 1980).
Spider collection

We sampled shrubs for spiders 5 times (in June and September of 2008 and 2009, and in June of 2010) using the beating-sheet method (Ehmann and MacMahon 1996), which consists in striking a shrub so that spiders fall directly on a sheet placed under the shrub and are quickly captured. This method captures about 84% of spiders on big sagebrush, and this rate represents an unbiased sample of species found on the shrubs (Ehmann 1994). Small spiders were caught with an aspirator and large spiders were captured by hand using vials. Although spiders in sagebrush habitat can recolonize empty shrubs within hours (Ehmann and MacMahon 1996), we ensured an interval of one month on average between sampling periods in a given year to maximize spider abundances on shrubs (Robinson 1981). We restricted sampling to warm days in the absence of wind and rain and immediately preserved all spiders in 70% ethanol for later identification to species. We pooled the species *Dictyna idahoana*, *Emblyna piratica* and *Emblyna reticulata* to consider them as one morphospecies, because juveniles were common and are difficult to identify to species (Chamberlin and Gertsch 1958).

Geographic and environmental factors

We took the geographic coordinates (Universal Trans-Mercator x-y-coordinates, in meters) from the center of each sampling location. Between 25 July and 27 July 2010, we estimated at each site the % cover of three vegetation categories representing different levels of structural complexity: woody plants, forbs and grasses. We used the line intercept method (Canfield 1941) to estimate % sagebrush cover (three 20 m transects per site) and the Daubenmire method (Daubenmire 1959) to estimate the % cover of non-
sagebrush woody plants, forbs and grasses (20 quadrats of 20 x 50 cm per site along 4 transects, all quadrats separated by 4 m or more to avoid sagebrush). To estimate differences in temperature regime across sampling locations, we placed two HOBO data loggers per site, which continuously and simultaneously recorded hourly temperatures between 30 July and 24 August 2010. Each logger was suspended 40 cm above the ground on a wooden stick, and covered with a Styrofoam cup. We averaged all the recordings to calculate average site temperatures.

Statistical analyses

We first ran 2-way analyses of variance (ANOVA) in R 2.10.1 (R Development Core Team 2011) to test for differences in spider density and species richness as a function of elevation and slope aspect. Response variables corresponded to pooled values over the five sampling periods to capture temporal variability in abundance and species richness. We expressed density and richness values relative to a volume representative of shrub size at our sites (0.1m³) and log₁₀-transformed these values to meet assumptions of normality. We ran a 1-way ANOVA for each elevation to identify the slope aspects responsible for significant differences in abundance and richness. Post-hoc pair-wise comparisons were done using Tukey’s Honestly Significant Difference test.

We examined differences in spider community composition across slope aspects at each of the three elevations, using analysis of similarity (ANOSIM). This non-parametric test does not rely on the assumptions of a MANOVA and is based on a rank permutation procedure of the R statistic, which tests the null hypothesis that there is no significant difference between treatments. The value of R determines the level of
difference between communities, such that \( R = 1 \) signifies total dissimilarity between groups and \( R = 0 \) indicates complete similarity. In order to include rare species and given that 86% of the genera we collected were represented by a single species, we performed analyses at the genus level. We omitted from the analyses rare genera that contributed less than 1% to the total abundance. In addition, we transformed data by a square root before analysis to downweight the importance of very common genera, and allow the rare genera to have some contribution (Clarke and Warwick 2001). We determined qualitative changes in community composition (variation in the identity of genera present) by comparing values of the Sørensen coefficient and quantitative changes (variation in the relative abundances of genera) by comparing values of the Bray-Curtis coefficient (Jost et al. 2011).

We used SIMPER similarity percentage analysis to identify those genera that contributed most to the dissimilarity between the two aspects that contained the most different spider assemblages at each elevation, based on the Bray-Curtis index. ANOSIM (using 10000 permutations) and SIMPER analyses were conducted using the PAST software package (ver. 2.09, Hammer et al. 2001). Where data were transformed for analysis, back-transformed data are shown in figures and tables.

To determine the relative importance of each environmental factor for cursorial and web spiders separately, we used multiple regression on distance matrices (MRM), a non-parametric method which assesses the relationship between species abundance distances and each of several environmental factors, represented by their own distance matrices (Lichstein 2007). Given that environmental factors were measured in July 2010, we restricted the analyses to the spider abundance data collected in June 2010. The
significance of the model and regression coefficients is tested by permuting the response matrix while the explanatory matrices are held constant. We standardized all the environmental variables to a mean = 0 and variance = 1 to give them equal weight and provide a consistent frame of reference for the coefficients (Goslee 2010). Then we converted the environmental and geographical data into individual distance matrices using Euclidean distances between pairs of sites for comparison with the Bray-Curtis dissimilarity matrix of spider composition.

We did not include % grass as a matrix variable in the multiple regression because it was strongly correlated to % cover of woody plants and forbs (Pearson’s product moment correlation, r = -0.75 and r = -0.50, respectively). Complete independence between explanatory matrices is rare; therefore we ran additional partial multiple regressions in which environmental matrices of interest were excluded to estimate the “pure effect” (Lichstein 2007) of each independent matrix expressed as a percentage of the variation explained by the whole model. All regressions were based on 10000 permutations. Analyses were performed in the statistical software package ECODIST (Goslee and Urban 2007) in R 2.13.1 (R Development Core Team 2011). Since ECODIST function MRM uses linear regression, we squared the dissimilarity values of spider composition prior to regression to improve linearity.

Results

Spider density

We collected a total of 16224 spiders. Both elevation and slope aspect significantly predicted spider density in shrubs (2-way ANOVA, $F_{2,228} = 458.6$, $P <$
and \( F_{3,228} = 18.86, P < 0.0001 \) respectively). Spider density was significantly different at each elevation (Tukey’s HSD, \( P < 0.0001 \)), peaking in shrubs at the mid-elevation (mean = 126.47), followed by the low (mean = 34.59) and high (mean = 18.74) elevations.

The effect of aspect differed between elevations (Fig. 2.2), as indicated by a significant interaction term (2-way ANOVA, \( F_{6,228} = 7.6, P < 0.0001 \)). Aspect was not related to abundance at the low elevation (ANOVA, \( F_{3,76} = 0.71, P = 0.54 \)). At the intermediate elevation, shrubs on S (mean = 157.03) and W (mean = 137.08) contained significantly higher spider densities than those on N (mean = 95.71), (ANOVA, \( F_{3,76} = 5.24, P = 0.002 \), Tukey’s HSD, \( 0.001 < P < 0.034 \)), but did not differ from E (mean = 124.45, Tukey’s HSD, \( 0.28 < P < 0.88 \)). At the high elevation, shrubs on W (mean = 29.17) and S (mean = 27.41) aspects had significantly higher spider densities than those on N (mean = 13.80) and E (mean = 11.19) (ANOVA, \( F_{3,76} = 27.08, P < 0.0001 \), Tukey’s HSD, \( P < 0.0001 \)).

Species richness

We found a total of 49 genera, comprising 61 spider species across all sites (Appendix, Table A.1). Both elevation and slope aspect significantly predicted spider species richness in shrubs (2-way ANOVA, respectively \( F_{2,228} = 52.72, P < 0.0001 \) and \( F_{3,228} = 13.02, P < 0.0001 \)). Species richness was significantly different at each elevation, with shrubs at the intermediate elevation containing the most species (mean = 12.07), followed by the low (mean = 9.74) and high (mean = 6.41) elevations (Tukey’s HSD, \( P < 0.01 \)).
The effect of aspect depended on elevation (Fig. 2.3), as indicated by a significant
interaction term ($F_{6,228} = 3.15, P = 0.005$). At the low elevation, W contained significantly
more species (mean = 12.91) than E (mean = 7.63) (ANOVA, $F_{3,76} = 5.05, P = 0.003$,
Tukey’s HSD, $P = 0.001$), but did not differ from N and S, which both had a mean
richness of 9.54 (Tukey’s HSD, $P = 0.12$). At the mid elevation, S yielded significantly
more species (mean = 16.86) than W (mean = 11.53), N (mean = 11.42), and E (mean = 9.54) (ANOVA, $F_{3,76} = 8.89, P < 0.0001$, Tukey’s HSD, $P \leq 0.006$). Finally, at the high
elevation, species richness was significantly higher on W (mean = 7.92) and S (mean = 7.55) compared to N (mean = 5.16) and E (mean = 5.45) (ANOVA, $F_{3,76} = 6.07, P < 0.001$, Tukey’s HSD, $0.005 < P < 0.05$).

Spider community composition

ANOSIM analyses provided compelling evidence of community differentiation
across aspects at each elevation. Quantitative differences were consistently greater than
qualitative differences (Table 2.1), indicating that dissimilarities in spider community
composition across aspects at a given elevation were due to relative changes in genus
abundance more than to genus turnover. Indeed, most of the genera occurred throughout
all 12 sites, and at each elevation, all aspects contained significantly different
communities when we ran analyses based on quantitative differences. Community
differences across aspects were strongest at the high elevation (ANOSIM, Sorensen $R = 0.381$, Bray-Curtis $R = 0.529, P < 0.0001$) and lowest at the intermediate elevation, with
virtually no differences in genus identity (Sorensen $R = 0.090$, Bray-Curtis $R = 0.235, P < 0.0001$). Pairwise comparisons revealed that at all elevations, the two slope aspects that
contained the most different spider assemblages always consisted in a “cold” aspect (N, E) and a “warm” aspect (S, W) (Table 2.1).

The SIMPER procedure revealed that the slope aspects with the most different communities at each elevation had an average dissimilarity of 41.26% (E and S, low elevation), 26.71% (N and W, mid-elevation) and 53.30% (N and S, high elevation). At each elevation, three to five genera explained close to 60% of the dissimilarity between aspects (Table 2.2). Community dissimilarities at the low elevation were primarily due to *Emblyna* tangle-web spiders and *Sassacus* jumping spiders, whereas those at the intermediate and high elevations were mainly shaped by *Pelegrina* jumping spiders and *Emblyna*. The slope aspect with the highest density of a given genus typically varied depending on the elevation (Table 2.2), as illustrated by *Pelegrina*, where highest densities occurred on “cold” aspects at the low and middle elevations but shifted to a “warm” aspect at the high elevation.

Multiple regression

The $R^2$ of the whole model revealed that our variables (Table 2.3) explained about half of the dissimilarity in guild species composition, with a better explanation of cursorial spider variation (65.1%) than of web spider variation (42.8%). The species composition of each spider guild was differently affected by the factors in our model (Table 2.4). Temperature alone accounted for much of the variation in cursorial assemblages (56.5%, MRM, $P = 0.0001$), whereas variation in web-builder assemblages was related to dissimilarity in woody cover (28.82 %, MRM, $P = 0.003$), followed by differences in temperature across sites (24.18 %, MRM, $P = 0.0026$). Dissimilarity in
woody cover across sites was not related to differences in cursorial community structure (0.092%, \( P = 0.83 \)). The remaining variables did not significantly contribute to community composition (Table 2.4).

**Discussion**

Trends in community structure along elevation gradients are well documented, but there still is no consensus on the mechanisms underlying these patterns (Lessard et al. 2011). It is critical to understand the origin of these discrepancies, because mountain ecosystems provide important opportunities for the conservation, management and prediction of future species assemblages by global warming (Lomolino 2001; Hodkinson 2005; Röder et al. 2010). We investigated the possibility that overall spatial patterns may be obscured by small-scale differences in topography and by pooling species that strongly differ in biological traits and requirements.

We found that despite relatively modest geographic distances between sites (\( \approx 500 \) m) within a given elevation, sites with different slope aspects could contain very different spider communities. Notably, the magnitude of variation in species abundance or richness across aspects at a given elevation was in some cases of greater magnitude than that across different elevations. For instance, mean species richness in shrubs on the east aspect/low elevation was not different from that on the south aspect/high elevation, whereas richness was significantly lower on the east aspect compared to the west within the low elevation.

Since climatic conditions become more extreme with increasing elevation (Geiger 1950), organisms that are strongly dependent upon fine-scaled environmental factors for
habitat choice may be particularly sensitive to the diverse environments resulting from topography. For instance, species distributions along elevation gradients have been linked to fine-scale variables in butterflies (Illan et al. 2010) spiders (Sattler et al. 2010), detrital arthropods (Lessard et al. 2011) toads (Moore et al. 2004), and small mammals (Orrock et al. 2000). Environmental differences over small spatial extents provide opportunities for individual organisms that are able to move short distances to escape unfavorable microclimates and shift to better ones (Sugitt et al. 2011). Therefore, fine-scale topographic effects cannot be ignored, and sampling at smaller extents may be critical to capture variation in the community composition of small organisms. We found that spider abundance and species richness were typically higher on south and west-facing slopes, especially at the highest elevation. Since temperature affects the growth, development and activity of arthropods (Hodkinson 2005), it is likely that the warmer conditions on these aspects provided ameliorating effects that enabled spiders to thrive at higher elevations.

In this study, species richness peaked at the intermediate elevation when richness values were pooled across aspects at each elevation. Mid-elevation humps in species richness are a well-known pattern in macroecology (Lomolino 2001) that has been documented in spiders (McCoy 1990; Chatzaki et al. 2005). Several hypotheses have been suggested to explain this pattern, including the higher chance for species ranges to overlap at mid-elevations (Sanders 2002), higher productivity at mid-elevations, and the contribution of predation and reduced resources to the limiting effects of climatic severity at lower and higher elevations (McCoy 1990). However, when each of our four slope aspects was considered separately at each elevation, it became apparent that the shape of
the elevational trend in species richness does not necessarily involve a mid-elevation peak, and that the pattern differs depending on which slope aspect is included.

The significant peak in spider abundances at the intermediate elevation is remarkable because species collected at the intermediate elevation also typically occurred at the low and high elevations. The low turnover in species identity with elevation may originate from the wide ecological tolerances of the species we collected. Indeed, species that drove the peak in abundance at the intermediate elevation and that were less common at the other elevations are known from wide geographic areas: the web-builders *Emblyna piratica* and *Emblyna reticulata* occur in the western USA down into Mexico (Chamberlin and Gertsch 1958), *Theridion petraeum* is a holarctic species (Levi 1957), the jumping spider *Pelegrina clemata* is found throughout western Canada and USA (Maddison 1996), and the lynx spider *Oxyopes scalaris* occurs in Canada down to Mexico (Brady 1964). Species with broad environmental tolerances may, nonetheless, have a strong dependence on the physical structure of the environment. At the intermediate elevation, woody plant cover was greater than at the other elevations, with more forb cover than at lower sites. Thus, vegetation at the mid-elevation was structurally more complex and likely provided a more diversified habitat than the vegetation at high and low elevations. Vegetation complexity has consistently been recognized as one of the most important factors in determining the presence of spider species (Hatley and MacMahon 1980; Wise 1993). By supporting more individuals, sites at the intermediate elevation may have supported more species via reduced probabilities of local extinction.

The peak in abundance at the intermediate elevation was most dramatic in *Emblyna piratica*. Since this relatively small species relies on vegetation extremities for
web construction, it may have been especially sensitive to the increased structural complexity provided by vegetation at the intermediate elevation. Web-building spider diversity along elevational transects in tropical and temperate locations are mainly determined by vegetation structure, compared to climate and prey availability (Greenstone 1984; Rypstra 1986). Higher spider abundances may have been further supported by the climatic conditions at the intermediate elevation, which are typically less extreme compared to those at higher elevations, particularly with respect to diel fluctuations (Geiger 1950).

The hypothesis that species distributions are patchy emphasizes that species communities are a mosaic where species composition is determined by environmental site characteristics, whereas the hypothesis that species composition fluctuates randomly predicts that community similarity decreases with increasing geographic distance due to dispersal limitation (Tuomisto et al. 2003; Sattler et al. 2010). We found that environmental variables accounted for higher proportions of the total variance in community composition than did geographic distances between sites. Dissimilarity in community structure was better explained by our model for cursorial spiders, perhaps indicating a stronger influence of stochastic processes behind web spider community composition. The higher spatial component for web spiders revealed by the partial MRM analyses may reflect competitive interactions with other spiders, whereby territoriality may have a stronger role in structuring the assemblages of web spiders compared to cursorial species.

While we did not include all the variables of importance to spiders, we found differing effects of environmental factors among spider guilds. Spatial variation in
temperature was the only driving variable behind the structure of cursorial assemblages, whereas vegetation structure and temperature had a dominant role in explaining web spider assemblages. Since web-building species require specific substrate configurations to build their webs (Hatley and MacMahon 1980; Marc and Canard 1997), the availability of appropriate structures for attaching a web is probably the most direct effect of vegetation complexity for web-builders (Jimenez-Valverde and Lobo 2007), although indirect effects of plant cover such as microclimate (Geiger 1950), prey availability and reduced competition (Sunderland and Samu 2000) may be related. In contrast, since microhabitat relocations are part of the foraging strategy of actively hunting spiders (Ford 1978; Wise 1993), cursorial species may not be as dependent on specific habitat structures as web spiders. For instance, Grill et al. (2005) found that cursorial spiders in Mediterranean shrubland were more strongly associated with moisture than with vegetation cover. Forb cover was not a significant predictor of community structure in web-builders, perhaps because herbaceous plants are more flexible and simpler in architecture than woody plants, thereby providing fewer and less desirable web sites.

The relatively stronger contribution of temperature to differences across cursorial communities (twice that of web spiders) may indicate a stronger dependence upon temperature for foraging efficiency. However, direct effects of temperature on hunting performance appear to be trivial in cursorial spiders compared to most insect prey, which experience decreased locomotion rates at lower temperatures (Schmalhofer and Casey 1999). Cursorial spiders that rely on vision (e.g. jumping spiders) may thus experience reduced foraging success at colder sites, because they are less likely to detect slow-moving prey (Tarsitano and Jackson 1992). Recent studies have suggested that patterns
of community composition differ among subsets of species based on differences in relevant traits and requirements (Marquet et al. 2004; Krasnov et al. 2010). Here, we demonstrate that foraging behavior may be a good approach to elucidate the mechanisms underlying spider diversity patterns.

Our results suggest that small-scale, topographically-induced site characteristics such as microclimate and vegetation structure can exacerbate the effects of broader-scale variation in the predictors of community structure along elevational trends. Impending climate change is increasing the need to solve the relationships between environmental factors and the composition of species assemblages along montane gradients. Given that species display a diversity of biological characteristics that affect how they perceive their environment, predicting community structure accurately relies on a good understanding of the natural history of species. Studies should gain efficiency in disentangling the mechanisms that drive patterns of species diversity by sampling at spatial scales that are biologically relevant to the organisms being considered, and by incorporating species differences in biological traits.

References


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Ehmann WJ (1994) The organization of shrub-steppe spider assemblages: a hierarchical evaluation of deterministic and stochastic influences. PhD dissertation, Department of Biology, Utah State University, Logan, Utah, USA


Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecol Lett 8:224-239


Table 2.1 ANOSIM results for comparisons of spider community structure on all aspects at a given elevation (global analysis) and on the two slope aspects that contained the most different spider assemblages at each elevation. R values range from R=0 (complete similarity between communities) to R=1 (total dissimilarity between communities).

<table>
<thead>
<tr>
<th>Composition measure</th>
<th>Elevation</th>
<th>ANOSIM R value</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Global</td>
<td>Most different pair</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sorensen (qualitative)</td>
<td>Low</td>
<td>0.156**</td>
<td>0.316** (N-S)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Intermediate</td>
<td>0.09**</td>
<td>0.234** (N-W)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.381**</td>
<td>0.559** (N-S)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bray-Curtis (quantitative)</td>
<td>Low</td>
<td>0.390**</td>
<td>0.711** (E-S)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Intermediate</td>
<td>0.235**</td>
<td>0.442** (N-W)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.529**</td>
<td>0.692** (N-S)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**, P < 0.001. Letters in parentheses indicate slope aspects (N, north, E, east, S, south, W, west).
Table 2.2 The percentage contribution of individual genera to pairwise dissimilarities between the two aspects that contained the most different spider assemblages at each elevation, based on the Bray-Curtis similarity index (SIMPER). Back-transformed genus densities (genus abundance/m$^2$) are listed for each understory treatment but the analyses were performed on square root-transformed numbers.

<table>
<thead>
<tr>
<th>Elevation</th>
<th>Genus</th>
<th>Dissimilarity (% contribution)</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>East-South North-West North-South</td>
<td>North East South West</td>
</tr>
<tr>
<td>Low</td>
<td><em>Emblyna</em></td>
<td>19.02 — — —</td>
<td>82.62 3.72 —</td>
</tr>
<tr>
<td></td>
<td><em>Sassacus</em></td>
<td>16.51 — — —</td>
<td>5.38 72.76 —</td>
</tr>
<tr>
<td></td>
<td><em>Pelegrina</em></td>
<td>12.93 — — —</td>
<td>136.89 48.3 —</td>
</tr>
<tr>
<td></td>
<td><em>Philodromus</em></td>
<td>11.64 — — —</td>
<td>5.61 43.56 —</td>
</tr>
<tr>
<td>Intermediate</td>
<td><em>Emblyna</em></td>
<td>— 28.03 — —</td>
<td>479.61 — — 942.49</td>
</tr>
<tr>
<td></td>
<td><em>Pelegrina</em></td>
<td>— 16.98 — —</td>
<td>275.56 — — 121</td>
</tr>
<tr>
<td></td>
<td><em>Oxyopes</em></td>
<td>— 14.23 — —</td>
<td>36 — — 81</td>
</tr>
<tr>
<td>High</td>
<td><em>Pelegrina</em></td>
<td>— — 19.49</td>
<td>20.43 — 118.81 —</td>
</tr>
<tr>
<td></td>
<td><em>Emblyna</em></td>
<td>— — 10.52</td>
<td>61.152 — 44.356 —</td>
</tr>
<tr>
<td></td>
<td><em>Dendryphantes</em></td>
<td>— — 9.64</td>
<td>10.049 — 0 —</td>
</tr>
<tr>
<td></td>
<td><em>Oxyopes</em></td>
<td>— — 9.44</td>
<td>0 — 10.563 —</td>
</tr>
<tr>
<td></td>
<td><em>Philodromus</em></td>
<td>— — 8.19</td>
<td>10.304 — 23.04 —</td>
</tr>
</tbody>
</table>
Table 2.3 Average temperature, minimum and maximum temperature, and percent cover of woody plants and forbs at each site. Temperature data were gathered 40 cm above the ground.

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>Aspect</th>
<th>Temperature (°C)</th>
<th>Cover (%)</th>
<th>Woody</th>
<th>Forb</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Average</td>
<td>Range (min, max)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1715</td>
<td>N</td>
<td>17.36</td>
<td>-2.30, 38.36</td>
<td>43.11</td>
<td>30.14</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>17.94</td>
<td>-2.83, 40.57</td>
<td>46.81</td>
<td>26.65</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>19.63</td>
<td>-0.59, 41.44</td>
<td>37.52</td>
<td>10.90</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>18.09</td>
<td>-1.58, 39.63</td>
<td>29.58</td>
<td>9.58</td>
</tr>
<tr>
<td>1915</td>
<td>N</td>
<td>18.14</td>
<td>-1.24, 37.64</td>
<td>57.28</td>
<td>17.80</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>17.99</td>
<td>-1.12, 37.20</td>
<td>60.91</td>
<td>17.98</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>18.19</td>
<td>-0.81, 38.42</td>
<td>46.43</td>
<td>11.06</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>17.94</td>
<td>-0.39, 39.82</td>
<td>62.52</td>
<td>17.42</td>
</tr>
<tr>
<td>2345</td>
<td>N</td>
<td>15.13</td>
<td>-4.46, 34.49</td>
<td>47.37</td>
<td>11.98</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>15.54</td>
<td>-4.22, 34.07</td>
<td>36.29</td>
<td>15.37</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>16.86</td>
<td>-0.84, 34.91</td>
<td>44.08</td>
<td>12.35</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>15.52</td>
<td>-3.62, 34.17</td>
<td>52.57</td>
<td>12.25</td>
</tr>
</tbody>
</table>
Table 2.4 Results of multiple regressions on distance matrices using a permutation method with the squared matrix of pairwise dissimilarity in spider genus composition (dependent matrix) and pairwise geographical and environmental distances between sites (independent matrices).

<table>
<thead>
<tr>
<th>Guild</th>
<th>Independent distance matrix</th>
<th>R² of the entire model</th>
<th>R² without an independent matrix</th>
<th>% of explained variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cursorial</td>
<td>Site location</td>
<td>0.650**</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.283*</td>
<td>56.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>% woody cover</td>
<td>0.650**</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>% herb cover</td>
<td>0.642**</td>
<td>1.39</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.651**</td>
<td></td>
</tr>
<tr>
<td>Web-building</td>
<td>Site location</td>
<td>0.396**</td>
<td>7.53</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>0.324*</td>
<td>24.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>% woody cover</td>
<td>0.304*</td>
<td>28.82</td>
<td></td>
</tr>
<tr>
<td></td>
<td>% herb cover</td>
<td>0.424**</td>
<td>0.93</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.428**</td>
<td></td>
</tr>
</tbody>
</table>

*, P value < 0.05; **, P value <0.001. See text for details about explained variation due to “pure” (i.e. completely independent) effects.
Fig. 2.1 Range (in degrees) of each slope aspect in this study. Instead of defining each aspect as one of four 90° sections (delimited by the two diagonal lines that intersect the circle) we restricted our aspects to 20° sections (colored sections) to reduce environmental overlap.
Fig. 2.2 Mean spider abundance per 0.1 m$^3$(volume representative of shrub size at our field sites) at each sampling location. Error bars represent one standard error, n=20 for each site. Means with different letters are significantly different (P < 0.05). Back-transformed data are presented but the analyses were performed on log$_{10}$-transformed numbers.
Fig. 2.3 Mean spider species richness per 0.1 m³ (volume representative of shrub size at our field sites) at each sampling location. Error bars represent one standard error, n=20 for each site. Means with different letters are significantly different (P < 0.05). Back-transformed data are presented but the analyses were performed on log_{10}-transformed numbers.
CHAPTER 3

GUILD MOBILITY PREDICTS SPIDER DIVERSITY: LINKS BETWEEN
FORAGING BEHAVIOR AND SENSITIVITY TO ADJACENT
VEGETATION STRUCTURE\textsuperscript{2,3}

Abstract

Modified vegetation structure strongly affects species distributions via changes in abiotic and biotic conditions, but the response of species may depend on how they exploit resources. Mobility and movement patterns, in particular, may affect the way organisms perceive their landscape, especially in the context of habitat change. It is likely that sedentary species perceive habitat features at smaller spatial extents compared to mobile species, but there is a lack of experimental research on the effects of fine-scale habitat characteristics on organisms of differing mobility. Spiders display two basic mobility levels based on foraging behavior: web-building species are sedentary and restricted to specific sites whereas cursorial species are mobile. We collected spiders inhabiting sagebrush shrubs with modified understory structures, to examine 1) whether habitat structure in the immediate vicinity of shrubs affected cursorial and web spiders differently in terms of abundance and species richness and 2) which genera most contributed to changes in community composition. Shrubs without understory had reduced cursorial spider densities and species richness compared to shrubs with added and unmodified understories, whereas web spiders lacked significant responses to

\textsuperscript{2} This chapter is co-authored by Stephanie M. Cobbold and James A. MacMahon.
\textsuperscript{3} This chapter is in review at Basic and Applied Ecology.
treatments. Community-level differences based on relative abundance of genera were detected in cursorial spiders but not in web spiders, despite a strong contribution of the web-building genus *Theridion* to community dissimilarities. Our results support the hypothesis that sedentary organisms may be sensitive to contiguous habitat at finer spatial scales than cursorial organisms, and highlight the risks associated with only collecting local habitat information when studying mobile species.

**Introduction**

Habitat structure has a major influence on the local distribution of species because it affects important abiotic and biotic habitat variables, including temperature, vapor pressure deficit, wind speed and light intensity (Geiger 1950), refuge availability, prey availability, and the intensity of competition and predation (Sunderland and Samu 2000). However, the composition of local species assemblages may also be driven by habitat characteristics at larger spatial extents, because species experience ecological processes that operate across a range of scales (Whittaker, Willis, & Field 2001). As a result, models of species distribution restricted to local environmental characteristics may be inadequate for most taxa (Mazerolle and Villard 1999).

Sensitivity to environmental characteristics beyond the local habitat is associated with particular biological traits, including large body size (Holland, Fahrig, & Cappuccino 2005), high mobility (Cole, Pollock, Robertson, Holland, McCracken et al. 2010), and large home range (Wiens, Crawford, & Gosz 1985). It follows that species may have distinct sensitivities to modifications in habitat structure depending on the scale at which these changes occur, and that determining the most appropriate spatial scale to
collect data should reduce the risk of missing important information on species-habitat interactions.

The effect of landscape heterogeneity on species composition may be particularly important for mobile organisms because they are likely to respond to features on a larger scale than less mobile species (Aviron, Burel, Baudry, & Schermann 2005; Holland et al. 2005). However, studies of this hypothesis typically consist in quantifying patterns in already-existing landscapes (e.g. Weibull & Ostman 2003; Dauber, Purtauf, Allspach, Frisch, Voigtlander et al. 2005; Cole et al. 2010), whereas manipulative experiments, which would be subject to fewer confounding variables, are lacking mostly due to the difficulty of conducting experiments at large spatial scales. Yet, habitat structure and its effects may also operate at smaller scales, especially for small organisms. Here, we provide research on spider communities inhabiting sagebrush shrubs (*Artemisia tridentata*) surrounded by modified habitat structures. Single shrubs represent discrete habitat patches for spiders, because individuals remain on the same shrub for days to weeks and form distinct communities in response to shrub characteristics (Wing 1984). Spider assemblages are suitable systems for evaluating how mobility affects the response of organisms to neighboring habitat structure, because spiders are abundant, diverse, and very sensitive to habitat structure and microclimatic conditions (Wise 1993), and can be classified into two guilds of differing mobility: sedentary spiders that use silk traps to catch their prey and hunters that actively pursue prey.

Web spiders and cursorial spiders may be differentially affected by vegetation structure in the vicinity of their habitat patch. First, the mobility of cursorial spiders provides them with greater flexibility to leave areas with low prey availability or
unfavorable microclimate (Samu, Sunderland, & Szinetar 1999), whereas site abandonment comes at a high energetic cost in sedentary spiders, which must build a new web (Tanaka 1989) and avoid predation during and after relocation (Lubin, Ellner, & Kotzman 1993). Second, since microhabitat relocations are part of the foraging strategy of actively hunting spiders (Ford 1978), they may use not only their immediate surroundings (e.g., a shrub), but also suitable habitats several meters away (Ehmann & MacMahon 1996; Sunderland & Samu 2000). In contrast, web spiders remain on their web and adopt a passive sit and wait foraging strategy. Given these guild differences, we tested the hypothesis that modifications of the vegetation structure in the vicinity of shrubs would generate within shrubs greater changes in the cursorial spider assemblage compared to the less mobile web spider community.

**Materials and methods**

**Experimental design**

We conducted this study at Woodcamp Hollow, Cache Co., Utah, on a south-facing slope dominated by big sagebrush (*Artemisia tridentata*), at an elevation of 1915 m. On July 25, 2010, a Daubenmire survey (Daubenmire 1959) established that the ground cover of the understory at this site consisted mainly of grasses (25.5%), followed by bare soil (18.5%), herbs (16.2%), and woody plants (7.3%). Herbs included littleleaf pussytoes (*Antennaria microphylla*), yarrow (*Achillea millefolium*), sticky geranium (*Geranium viscosissimum*), meadow thistle (*Cirsium scariosum*), oneflower helianthella (*Helianthella uniflora*) and sego lily (*Calochortus nuttallii*). Woody plants in the
understory consisted mainly of rubber rabbitbrush (*Chrysothamnus nauseosus*) and young sagebrush.

We randomly selected 60 sagebrush shrubs following criteria of size, shape and isolation (Ehmann & MacMahon 1996). Shrubs were at least 6 m apart, with canopies that ranged between 40 cm and 100 cm in any one dimension, to standardize the amount of substrate available to spiders and the likelihood of aerial colonization (Hatley & MacMahon 1980). On July 1 and July 2, 2010, we randomly assigned 20 shrubs to one of 3 treatments of their understory. We define shrub understory as the vegetation located within a 115 cm radius from the trunk of the shrub (Fig. 3.1). Relative to observed ground dispersal distances in spiders (Sunderland & Samu 2000) and given that both guilds are capable of aerial and terrestrial dispersal in sagebrush steppe (Ehmann 1994), we felt that these understory dimensions would create appreciable differences in shrub neighborhood across treatments, while ensuring that spiders could readily encounter the shrubs regardless of their mobility or colonization strategy.

The understory of 20 shrubs was left unmodified to serve as a control (Fig. 3.2A). The addition treatment consisted in adding 6 artificial structures or “modules” to the existing understory of 20 shrubs (Fig. 3.2B). We left enough space between adjacent modules to preserve the structure of any relatively large herbs or clumps of grass in the understory. Modules were made of chicken wire (2.5 cm mesh) externally and of 3 ply macramé jute internally. These materials have been used in previous studies of habitat preference in sagebrush habitat and are readily used by cursorial and web spiders (Robinson 1981; Cobbold & Supp, in press). Modules measured 45 x 45 x 23 cm and contained equal amounts of jute, strung vertically at the same density. Lastly, the removal
treatment consisted in eliminating the understory of 20 shrubs so that the soil was entirely exposed (Fig. 3.2C). We regularly inspected removal shrubs to ensure that they remained free of understory vegetation during the study.

In sagebrush habitat, habitat characteristics that are detrimental to spiders are also likely to negatively affect their prey, and both guilds use the herb stratum for habitat and dispersal between sagebrush shrubs (Abraham 1983). As a result, vegetation in close proximity to a shrub, such as the herb stratum, may 1) act as a reservoir from which species are able to disperse and potentially colonize shrubs and 2) provide microclimatic conditions near the shrub that affect the presence of species depending on their environmental requirements. A lack of vegetation near a shrub may increase its isolation from other shrubs and generate a harsher microclimate (Geiger 1950), which may deter ground and herb-dispersing species and decrease spider abundances in the shrub. In contrast, denser and more heterogeneous vegetation near a shrub should encourage the colonization of a more abundant and diverse spider fauna on the shrub, by providing buffering effects on temperature and humidity (Geiger 1950) and substrate that may facilitate non-aerial forms of spider dispersal (Samu et al. 1999).

Spider collection

We sampled shrubs for spiders 4 times between July 21, 2010 and September 13, 2010 using the beating-sheet method (Ehmann & MacMahon 1996), which consists in striking a shrub so that spiders fall directly onto a sheet placed under the shrub and are quickly captured. Spiders collected using this method on big sagebrush represent an unbiased sample of species found on the shrubs (Ehmann 1994). Although spiders in
sagebrush habitat can recolonize empty shrubs within hours (Ehmann & MacMahon 1996), we ensured an interval of 16 days on average between sampling periods to maximize spider abundances, as recommended by Robinson (1981). We restricted sampling to warm days in the absence of wind and rain. For shrubs in the addition treatment, we removed the modules to allow an efficient use of the beating sheet, after which we vigorously shook the modules 30 times to remove any spiders and replaced them in their original positions. All spiders were immediately preserved in 70% ethanol for later identification to species and to guild, based on their general foraging technique (Wise 1993): web-spinners are sedentary spiders that rely on silk constructions to catch prey, whereas cursorial or mobile spiders actively hunt their prey.

Statistical analyses

We used data over the four sampling periods combined for all analyses because a single sampling period may have yielded spider abundances that were too low for statistical analysis (Robinson 1981). We first ran multivariate analyses of variance (MANOVA) in R 2.13.1 (R Development Core Team 2011) to test for differences in spider density and species richness between each major spider guild (cursorial and web builder) across understory treatments. We expressed density and richness values relative to a volume representative of shrub size at our site (0.1m$^3$) and log$_{10}$-transformed these values to meet assumptions of normality. We ran post-hoc pair-wise comparisons using Tukey’s Honestly Significant Difference test.

We examined differences in spider composition across understory treatments for the whole community and for each guild separately, using analysis of similarity
(ANOSIM). This non-parametric test does not rely on the assumptions of a MANOVA and is based on a rank permutation procedure of the R statistic, which tests the null hypothesis that there is no significant difference between treatments. The value of R determines the level of difference between communities, such that $R = 1$ signifies total dissimilarity between groups and $R = 0$ indicates complete similarity. In order to include rare species and given that almost all genera were represented by a single species, we performed analyses at the genus level. We omitted from the analyses rare genera that contributed less than 1% to the total abundance. In addition, we used a square-root transformation before analysis to downweight the importance of very common genera, and allow the rare genera to have some contribution (Clarke & Warwick 2001). We determined qualitative changes in community composition (variation in the identity of genera present) by comparing values of the Sørensen coefficient and quantitative changes (variation in the relative abundances of genera) by comparing values of the Bray-Curtis coefficient (Jost, Chao, & Chazdon 2011).

We used SIMPER similarity percentage analysis to identify those genera that contributed most to the dissimilarity across treatments. ANOSIM (using 10000 permutations) and SIMPER analyses were conducted using the PAST software package (ver. 2.09, Hammer, Harper, & Ryan 2001). Where data were transformed, back-transformed data are shown in figures and tables.
Results

Spider density

The effect of understory treatment on spider density varied between guilds (MANOVA, Pillai’s $F_{4,114} = 4.48, P = 0.002$, Fig. 3.3A). Cursorial spiders on shrubs with removed understories were in significantly lower densities (mean = 10.8) compared to the unmodified (mean = 17.9) and addition (mean = 20.7) understory treatments, which did not differ from each other (ANOVA, $F_{2,57} = 10.34, P = 0.0001$, Tukey’s HSD, $P < 0.05$). In contrast, web spider density did not respond to understory treatment (ANOVA, $F_{2,57} = 0.59, P = 0.55$).

Species richness

The number of species collected on sagebrush was very similar in each spider guild (16 cursorial, 15 web-building). Shrubs contained between 2 and 9 cursorial species and between 2 and 8 web-building species. There was a marked difference in the response of cursorial and web-building species to understory treatment (MANOVA, Pillai’s $F_{4,114} = 2.85, P = 0.026$, Fig. 3.3B). The richness of cursorial spiders was significantly higher on shrubs with unmodified understories (mean = 5.05) compared to the removal (mean = 3.25) and addition (mean = 3.68) understory treatments (ANOVA, $F_{2,57} = 5.16, P = 0.008$, Tukey’s HSD, $P < 0.05$). In contrast, web spider richness did not respond to understory treatment (ANOVA, $F_{2,57} = 0.55, P = 0.57$).

Spider community composition

We found no difference in qualitative spider composition (presence-absence of genera) between treatments, as suggested by a low R statistic indicating high faunal
similarity (ANOSIM, $P = 0.053$, $R = 0.040$). However, quantitative community composition tests produced a higher global $R$ value (ANOSIM, $P = 0.0001$, $R = 0.103$), indicating a significant difference in relative spider density across treatments. Nevertheless, $R = 0.103$ suggests that these differences were relatively small. Pairwise comparisons revealed moderate but significant differences between the removal treatment and the two other treatments (removal-control: $P = 0.0035$, $R = 0.106$, removal-addition: $P = 0.0001$, $R = 0.149$). There was no difference between the control and addition treatments ($P = 0.059$, $R = 0.054$). These results suggest that differences in spider community composition across treatments were more due to relative changes in genus abundance than to genus turnover.

A separate analysis on each guild based on Bray-Curtis similarity indices revealed that the cursorial spider community was significantly different across all understory treatments and that these differences were relatively small (ANOSIM, $P = 0.0002$, $R = 0.106$). In contrast, the web spider community showed no trend across treatments (ANOSIM, $P = 0.63$, $R = 0.01$).

The SIMPER procedure revealed that the two significantly different treatment pairs (removal-control, removal-addition) indicated by the ANOSIM test had an average dissimilarity of 36.14% and 34.34% respectively (Table 3.1). With the exception of *Theridion*, web spider genera occurred in the lower part of Table 3.1, indicating that community dissimilarities across understory treatments were primarily due to cursorial genera. The five most discriminating genera, which explained close to 50% of the dissimilarity between the removal treatment and the other two treatments, were *Theridion*, followed by *Pelegrina, Oxyopes, Synageles* and *Philodromus*. In agreement
with our findings on cursorial guild densities (Fig. 3.3A), these genera all showed evidence of a decline in density between the addition and removal treatments, and, with the exception of *Pelegrina*, between the control and removal treatments (Table 3.1).

**Discussion**

Differences in the composition of local communities may be caused by ecological processes acting at larger spatial scales, but not all species are equally affected (Weibull & Ostman 2003; Dauber et al. 2005). Therefore, changes in selective pressure generated by modifications of the surrounding landscape may cause identical habitat patches with distinct surroundings to differ in species composition and community structure. In this experimental study, we collected shrub spiders of contrasting mobility to investigate the effects of neighboring habitat structure on community composition.

As predicted, guild and community differences across treatments were driven by cursorial spiders, despite a strong contribution of the web-building genus *Theridion* to community dissimilarities. We found markedly reduced cursorial spider densities in shrubs without understory, and more cursorial species in control shrubs, whereas web spiders lacked any significant response to treatments. The contrasting responses of the two spider guilds suggest that foraging behavior may mediate the outcome of surrounding habitat modifications on the local composition of spider communities. More generally, our findings support those studies which suggest mobility as a predictor of sensitivity to ecological processes acting at larger spatial scales (Jennings & Pocock 2009; Cole et al. 2010).
By enhancing prey habitat and microclimate stability (Cloudsley-Thompson 1962; Uetz 1979), vegetation structure in the vicinity of a habitat patch has important ecological consequences on predators within the patch, and can facilitate the movement of species through the landscape by reducing patch isolation (White, Antos, Fitzsimons, & Palmer 2005). Our finding that shrubs surrounded by bare soil supported simplified communities compared to control and addition shrubs agrees with a positive correlation between spider abundance and diversity with environmental diversity (Coyle 1981). Since modules efficiently attract cursorial and web spiders (Robinson 1981), the lack of significant community differences between our control and addition treatments may appear somewhat surprising. It is possible that our modules did not significantly enhance the density or heterogeneity of the natural understory.

Unlike sedentary species, mobile species are expected to exploit not only their immediate surroundings (e.g., a sagebrush shrub) but also suitable habitat in their close proximity. The use of both the herb and shrub layers by most spider species in our system (Abraham 1983; pers. obs.) probably played an important role in the development of different spider communities across understory treatments, in that the herb/module layer acted as potential source areas for shrubs. For instance, in a study by Costello and Daane (1998), the similar spider richness and abundance on vines with and without ground cover may be partly attributable to the lack of spider movement that they observed between the ground cover and the vines.

The stronger effect of neighboring vegetation on cursorial spiders compared to web spiders suggests that individual shrub traits may not be enough to describe the habitat characteristics of mobile spiders collected in shrubs. Yet, studies of habitat
preference typically collect habitat data at the same spatial extent for all species. Studies on spider-habitat associations often restrict their focus to the characteristics of the individual plants in which the spiders were found (e.g., Robinson 1981; Ehmann 1994), and studies of carabid habitat preference typically collect habitat information from directly adjacent to the pitfall traps (Bhriain, Skeffington, & Gormally 2002), often within < 0.3 m (Cole et al. 2010). However, if different species respond to their environment at their own spatial scale, then it becomes apparent that habitat information should be collected at the appropriate scale for the species under investigation (Cole et al. 2010). Even small-scale investigations of arthropod-habitat interactions should collect habitat data at larger spatial extents for mobile species to avoid missing important information.

The strong contribution of the web-building genus Theridion to community dissimilarities suggests possible effects of our understory treatments on local (i.e., shrub) conditions. One would expect sedentary spiders to be more sensitive to local changes compared to mobile spiders that use larger areas (Jennings & Pocock 2009). Given the known effects of ground vegetation on local temperature, humidity and wind (Geiger 1950), it is conceivable that our understory treatments generated within shrubs microclimatic changes to which Theridion was sensitive. Compared to other web spider genera in our system, most Theridion were immature and small, which may have increased their vulnerability to thermal and desiccation stress (Savory 1964), and decreased their densities on removal shrubs.

A caveat with respect to interpreting the data is that we did not pinpoint the specific mechanisms behind the response of spiders to the understory treatments. Spider
densities in a habitat patch are determined by multiple factors, including site selection (immigration), site-related rates of survival and reproduction, and site abandonment, which in turn are determined by various abiotic and biotic factors (Samu et al. 1999). Further experiments in controlled environments may provide the opportunity to gain more insights into the immediate causes of our findings. In addition, research over larger spatiotemporal extents would help evaluate the constancy of patterns, because not all species exhibit short-term responses to habitat change (Ewers & Didham 2006).

It seems reasonable to postulate that the decline in cursorial spiders on removal shrubs was due in large part to a loss of the ameliorating effects of neighboring vegetation on the microclimate near the ground. Our study demonstrates the role of adjacent habitat structure in promoting more complex local communities, and provides support for the role of mobility behind a more rapid response of species to changes in neighboring habitat structure. Recognizing the role of biological traits on community composition should improve our approach to collecting species habitat data. There is a growing interest in determining which habitat characteristics of agroecosystems favor pest predators such as spiders (Costello & Daane 1998; Silva, Franco, Vasconcelos, & Branco 2010; Simon, Bouvier, Debras, & Sauphanor 2011), and ground cover management has become a popular component of integrated pest management (Ingels, Bugg, McGourty, & Christensen 1998). More generally, effective conservation efforts on diverse taxonomic groups depend on a good understanding of the links between the biological characteristics of species and their sensitivity to habitat change.
References


Table 3.1. The percentage contribution of individual genera to pairwise dissimilarities between the control, addition and removal treatments based on Bray-Curtis similarity indices (SIMPER). Back-transformed genus densities (genus abundance/m²) are listed for each understory treatment but the analyses were performed on square root-transformed numbers.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Guild</th>
<th>Dissimilarity (% contribution)</th>
<th>Density</th>
<th></th>
<th></th>
<th></th>
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<tr>
<td></td>
<td></td>
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<td>A-R</td>
<td>C-A</td>
<td>Control</td>
<td>Addition</td>
</tr>
<tr>
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<td>13.75</td>
<td>11.26</td>
<td>48.30</td>
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<td>25.00</td>
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<td>0.77</td>
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</tr>
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</table>

C, Control; R, Removal; A, Addition.
**Fig. 3.1.** Definition of shrub understory in this study. The dark disk and the grey shape represent the trunk and the edge of the shrub foliage respectively.
Fig. 3.2. The three experimental treatments of the shrub understory: control (A), addition (B), and removal (C).
**Fig. 3.3.** Mean cursorial and web spider density (A) and species richness (B) per 0.1 m$^3$ (volume representative of shrub size at our field site) in the three understory treatments. Error bars represent one standard error, n=20 for each treatment. Back-transformed data are presented but the analyses were performed on log$_{10}$-transformed numbers.
CHAPTER 4

PATCH SHAPE ALTERS SPIDER COMMUNITY STRUCTURE: LINKS BETWEEN MICROHABITAT CHOICE AND SENSITIVITY TO INCREASED EDGE HABITAT

Abstract

Increased edge effects in fragmented habitats can affect the abundance of edge-dwelling organisms, but these impacts may depend on the biological attributes of species. Microhabitat choice, a species characteristic that reflects combinations of biological traits, may affect the ability of peripheral species to take advantage of increased edge habitat in the presence of edge effects. In this field study, we built artificial shrub modules designed to encourage web spiders to build webs on the periphery. While modules were identical in volume, they differed in shape (cubic and elongated), so that elongated modules had more edge habitat and were subject to enhanced edge effects. Given that the tangle-web spiders *Theridion* and *Dictyna* built webs on module edges and strongly differed in terms of concealment and substrate generalization, two habitat characteristics associated with lower vulnerability to habitat modification, we tested the hypothesis that *Theridion*, which built webs in more concealed locations and on a greater diversity of substrate configurations in the modules compared to *Dictyna*, would take better advantage of increased edge habitat. As predicted, *Theridion* was significantly

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4 This chapter is co-authored by Stephanie M. Cobbold and Sarah. R. Supp.
5 This chapter has been accepted for publication and is in press at the Journal of Insect Conservation (DOI 10.1007/s10841-011-9443-2). Copyright release with kind permission of Springer Science and Business Media.
more abundant on elongated modules whereas the abundance of *Dictyna* did not respond to shape, even though the change in module shape entailed a similar increase in favored substrate for both spider groups. Our results suggest that the microhabitat associations of organisms may be linked to their propensity to be sensitive to edges, and that a better understanding of these links can improve our ability to predict the effects of habitat modification on biodiversity.

**Introduction**

Increased habitat edge, one of the most important consequences of habitat fragmentation, fuels a diversity of edge effects on organisms, including changes in microclimatic conditions, nutrient cycling, dispersal rates, and predation pressure (Murcia 1995). While some organisms benefit from such edge effects, many are negatively affected in terms of foraging, movement, and survival (Burkey 1993; Ostman et al. 2009). Since increased edge habitat provides a greater exchange surface between a habitat patch and its surrounding environment, expanded peripheral habitat facilitates new interactions between species (Fagan et al. 1999), especially if resources are abundant along edges (Johnston and Odum 1956). For instance, predation efficiency can be greater on habitat patches that have more edge (Andren and Angelstam 1988; Sisk and Battin 2002), because such patches are more likely to be discovered, as predicted by the target area hypothesis (Gilpin and Diamond 1976; Lomolino 1990). Modified interactions may be beneficial or detrimental to edge organisms depending on their ecology, thereby affecting their ability to take advantage of increased edge habitat.
Edge vulnerability is associated with particular biological characteristics, including large body size and low ecological plasticity (Brand 2004), large home range (Wiens et al. 1985), poor mobility (Ewers and Didham 2006) and vulnerability to predation (Ries and Sisk 2010). However, information on life-history traits that could predict the effects of fragmentation is not always available, such as for the taxonomically diverse arthropods (Ewers and Didham 2006). In addition, species traits are strongly intercorrelated and can interact with each other to increase susceptibility to fragmentation (Ewers and Didham 2006). Under these circumstances, a characteristic such as microhabitat preference may be a useful predictor of fragmentation sensitivity, because habitat requirements reflect complexes of biological characteristics, some of which may be linked to edge sensitivity.

Growing rates of habitat fragmentation throughout the globe are increasing the need to understand how alterations of patch shape may interact with community structure via ecological changes at the edge of habitats. Here, we provide research on a spider community inhabiting experimental shrub modules of identical volume but different shape, where elongated modules have more edge habitat and are thus subject to enhanced edge effects. While habitat modification and its effects are often documented at relatively large spatial scales (meters to kilometers), these effects also operate at smaller scales, especially for small organisms. For instance, single shrubs represent discrete habitat patches for arid-land spiders, because individual spiders remain on a same shrub for days to weeks (Wing 1984) and form distinct communities in response to shrub characteristics (Chew 1961). Spider assemblages are suitable systems for evaluating the effects of habitat geometry on species abundances because spiders are abundant and diverse (Wise
1993) and have well-defined preferences for locations and structures within habitat patches (Hatley and MacMahon 1980; Marc and Canard 1997). Web spiders at habitat edges are expected to experience frequent species interactions because they are key predators that use webs to extend their range of influence, and because they are also prey to a large number of organisms including other spiders (Foelix 1996; Wise 2006). Accordingly, web spiders should be sensitive to the changes in species interactions that result from increased edge habitat.

The microhabitat choice and response of spiders to increased peripheral habitat may be influenced by their behavioral adaptations and life history traits. For instance, reduced concealment may relate to predation risk because it increases the likelihood of detection or capture (Caley and St John 1996, Manicom et al. 2008). Edge sensitivity in web spiders may be further exacerbated if species display other risk characteristics that increase vulnerability to habitat modification in general (Ewers and Didham 2006).

We focused on two web-building spider genera, *Theridion* (Theridiidae) and *Dictyna* (Dictynidae), which occupy similar ecological niches but differ in microhabitat choice in our modules. Elongated modules, which have more surface area than cubic modules of the same volume, are more likely to intercept organisms from the outside, and have an edge substrate that is more likely to be detected by organisms from within (Fig. 4.1), thereby fostering more species interactions at the edge compared to cubic modules. Given that *Theridion* and *Dictyna* inhabit the edges of our modules, we tested the hypothesis that when edge habitat was increased, differences in web site choice would alter the tangle-web spider community in favor of *Theridion*, the genus whose microhabitat characteristics have been linked to lower edge vulnerability.
Materials and methods

Experimental design

We built 20 cubic modules and 20 elongated modules, identical in volume (97336 cm³) and height (46 cm). Cubes were 46 cm wide (surface area of 12696 cm²) and elongated modules were 46 x 23 x 92 cm (surface area of 14812 cm²; Fig. 4.2). Modules were made of chicken wire (2.5 cm mesh) externally and of 5 ply macramé jute internally, as used in previous studies of habitat preference (Robinson 1981; Ehmann 1994b). This design efficiently attracts Theridion and Dictyna to shrub module edges, most likely because chicken wire offers more suitable attachment points for 3-dimensional webs, by comparison with the thicker, sparser and structurally simpler arrangement of the jute. Each module shape received the same amount of jute, strung vertically and horizontally at the same density, and all jute extremities were knotted to the chicken wire. We used plastic cable ties at the edges to secure the chicken wire and trimmed the ties as short as possible.

We conducted this study at the Utah State University Green Canyon Field Station, Cache Co., Utah (Lat. 41°45’59”N, Long. 111°47’11”W, elevation 1497 m). Vegetation was sagebrush steppe, dominated by Artemisia tridentata. We placed the modules on the ground amid the sagebrush shrubs, in a checkerboard pattern of 5 rows and 8 columns so that cubes and elongated modules alternated in the landscape. Modules were positioned to be the same height and were randomly assigned an orientation and secured with two small aluminum stakes. The spacing between modules ranged from 4 to 6 m.

Theridion (Theridiidae) and Dictyna (Dictynidae) are web spider genera that inhabit shrubs and that readily colonize artificial shrub modules made of jute and chicken
wire (Robinson 1981; Ehmann 1994b), making them ideal for an experimental study on the impacts of patch shape. These genera are ecologically similar since both build 3-dimensional webs at the extremities of vegetation (Marc and Canard 1997). In addition, the species at our site, *Theridion petraeum, Theridion sp. nov.* and *Dictyna idahoana* are similar in size, measuring between 2 mm and 3.5 mm in body length (Levi 1957; Chamberlin and Gertsch 1958; pers. obs.). However, *Theridion* typically suspends its web beneath covering objects (Benjamin and Zschokke 2002) or in shelters such as leaf retreats (Stiles and Coyle 2001; Manicom et al. 2008) whereas the webs of *Dictyna* are readily built in more exposed locations, resulting in flatter webs with most of the silk in a single plane (Jackson 1977; Pearson 2009). While exposed webs may intercept prey more frequently, 3-dimensional webs (Blackledge et al. 2003) and concealed webs (Manicom et al. 2008) provide better protection against detrimental encounters.

Visual inspections

We visually inspected the modules twice to verify whether the webs of *Theridion* and *Dictyna* 1) were consistently located on the periphery of the modules (i.e., attached to the chicken wire and spanning less than half the width of a module) and 2) differed in microhabitat characteristics that are known to affect sensitivity to modified edge habitat. We considered webs immediately surrounded by the most substrate, such as webs within a structure (e.g. cable tie) or at the junction of multiple or thick substrates (e.g. where the jute attached to the chicken wire) more concealed than webs built in visually more exposed locations, such as webs built on thin substrates (e.g. chicken wire alone) or on the side of the module. Although spiders in sagebrush habitat can recolonize empty
shrubs within hours (Ehmann and MacMahon 1996), we ensured an interval of 14 days between inspections to maximize spider abundances on modules, as recommended by Robinson (1981). Each time we found an occupied web, we recorded its location in the module specifying which substrate it was attached to, and identified the spider within it, after which we removed the web and its occupant. Unoccupied webs were destroyed but not recorded. After recording all webs in a module, we struck the module at least 30 times to remove any remaining spiders and replaced it in its original position for recolonization.

Web counts were meant to help interpret results from the module sampling (see below) rather than to document spider abundances because spider detection and capture via visual inspection is less efficient than via the beating-sheet technique (Ehmann 1994a), which we completed independently. With the latter method, modules are struck so that spiders fall directly on a sheet placed under the module and are quickly captured. Spiders captured using this method on big sagebrush represent an unbiased sample of species found on the shrubs (Ehmann 1994c). In contrast, during visual searches, spiders may drop out of their webs, and small or hidden webs may be more difficult to detect, resulting in less reliable spider counts.

Module sampling by beating-sheet technique

We placed both sets of modules on 24-May-2009 for colonization and sampled them for spiders between 16-Jun-2009 and 4-Aug-2009. We used the total abundance of spiders per module across 4 sampling periods as the response variable for each family, because a single sampling period may have yielded spider abundances that were too low
for statistical analysis at the family level (Robinson 1981). We completed each sampling period every 18 days on average and restricted sampling to warm days in the absence of wind and rain. All spiders were collected using the beating-sheet technique (Ehmann 1994a) and immediately preserved in 70% ethanol for later identification to species.

To estimate the potential for modified interactions between our web spider genera and other species at the edge of our modules, we also recorded the abundances of jumping spiders (Salticidae) and lynx spiders (Oxyopidae) at each sampling period to compare them to that of theridiids and dictynids. The noticeable abundance of salticids and oxyopids during our visual inspections, combined with their active hunting style and araneophagic behavior (Cutler et al. 1977; Jackson and Pollard 1996; Nyffeler 1999), led us to expect that they likely have strong interactions with *Dictyna* and *Theridion*. Salticids in particular feed on both moving and motionless prey (Nyffeler 1999), including spiders in their webs (Jackson and Pollard 1996; Ross 2008).

Statistical analyses

For each module shape, we ran a Cochran-Mantel-Haenszel (CMH) chi-square analysis of association to test the null hypothesis that genus identity and substrate choice were conditionally independent in each individual module. CMH tests compared the abundances of spider webs for each genus (*Theridion, Dictyna*) on each substrate type (wire, combination of wire and jute).

We performed a permutational multivariate analysis of variance based on distance matrices using the ADONIS function in the statistical software package VEGAN 1.17-1 (Oksanen et al. 2010) in R 2.10.1 (R Development Core Team 2009) to examine possible
differences in family abundance between the two module shapes over the four sampling periods combined. ADONIS is directly analogous to a multivariate analysis of variance (MANOVA) but does not assume parametric data. Significance tests in ADONIS were done using the $F$-test based on sequential sums of squares from permutations of the raw data. The pairwise distances between replicates were calculated with the Morisita-Horn dissimilarity index, which is based upon abundance data and is less dependent upon sample size and diversity than other quantitative indices (Wolda 1981). We ran follow-up 2-tailed Wilcoxon rank-sum tests to determine which spider families were responsible for significance.

**Results**

**Web counts**

We found 196 occupied webs over the two visual inspections, all of which were at least partially attached to the chicken wire, and rarely spanning 10 cm in any one dimension, thus demonstrating their peripheral location within modules. We did not find any webs attached to jute only. Webs contained either *Theridion* or *Dictyna*, except for three which contained immature *Metepeira foxi* (Araneidae). Webs could be assigned to 5 categories of concealment, based on their location within the module and the type of substrate to which they were attached (Table 4.1).

CMH chi-square tests on the abundance of webs at each substrate type revealed a significant association between spider genus and substrate choice (wire, combination of wire and jute) in cubic modules ($X^2 = 23.19$, df = 1, $P < 0.001$) and elongated modules ($X^2 = 13.91$, df = 1, $P < 0.001$). *Theridion* webs were most often attached to wire and jute.
(104 webs, Fig. 4.3a, 4.3b, Table 4.1), a combination that provides better cover than wire alone because jute is appreciably thicker than wire. In contrast, Dictyna webs were exclusively attached to wire alone (Figure 4.3c, 4.3d), indicating the microhabitat of this genus was more exposed and substrate-specific compared to that of Theridion. When Theridion built on chicken wire alone (50 webs) they did so mostly at the junction of the sides of modules (i.e. “ridge”, Table 4.1), and exposure was reduced 1) by centering the web on the plastic cable ties which were used as a retreat, especially by immatures (Fig. 4.3a) and 2) by building webs on the bottom ridges of modules, which were in contact with the ground and thus less exposed than the other ridges.

Given that Theridion built webs on wire and on adjacent jute whereas Dictyna built webs on wire only, we estimated the gain in preferred substrate for each genus on the rectangular module compared to the cube, by calculating the surface area of chicken wire and adjacent jute (jute strands and knots that are in contact with or adjacent to wire relative to the rest of the jute) on the 2 module shapes. We found that the gain in substrate for Theridion and Dictyna was almost identical (16.9% and 16.6%, respectively), despite their different substrate preferences.

Module sampling

The four most abundant spider families were Theridiidae (342 specimens), Salticidae (173 specimens), Dictynidae (109 specimens) and Oxyopidae (65 specimens). These families represented most of the module community (89.5 % of all collected spiders). Thus, theridiids and dictynids were the most abundant web spiders on our modules, whereas salticids and oxyopids, which are visually-guided predators (Wise
1993), were the most abundant cursorial spiders. We collected *Oxyopes scalaris* (Oxyopidae), a species known to prey on Theridiidae and several other spider families (Cutler et al. 1977), members of the salticid genera *Sassacus, Habronattus, Pelegrina* and of the web-invading genus *Phidippus* (Jackson and Pollard 1996), and *Mimetus* (Mimetidae), which specialize on web-building spiders (Ubick et al. 2005). Theridiids belonged exclusively to the genus *Theridion* except for one *Latrodectus hesperus*, and consisted of *Theridion petraeum* and *Theridion sp. nov.* (undescribed species, H. W. Levi pers.com.). Dictynids were exclusively represented by *Dictyna idahoana*, although some immatures were not identifiable to species. Theridiids were significantly more abundant on elongated modules than on cubic modules (ADONIS, $F = 5.420$, $R^2 = 0.124$, $P = 0.028$, Wilcoxon rank-sum test, $Z = -2.741$, $P = 0.006$), with a median abundance of 5.5 on cubes and 11 on elongated modules (Fig. 4.4). In contrast, dictynids did not show any significant difference in abundance as a function of module shape (Wilcoxon rank-sum test, $Z = 0.646$, $P = 0.518$), and neither did salticids (Wilcoxon rank-sum test, $Z = 0.412$, $P = 0.680$) or oxyopids (Wilcoxon rank-sum test, $Z = 0.251$, $P = 0.801$).

**Discussion**

Patch geometry is considered an ecologically important factor because the abundance of edge-dwelling species should increase with habitat shape complexity (Ewers and Didham 2007). However, an increase in edge habitat may not allow all edge-dwelling species to increase comparably. Instead, patch shape may select for species with traits that allow them to either evade or take advantage of the changes that typically occur with increases in edge-habitat, such as modified species interactions (Andren and
Angelstam 1988; Sisk and Battin 2002; Ewers and Didham 2006). Accordingly, changes in selective pressure generated by alterations in patch shape may cause patches of same size but of different shape to differ in species composition and community structure.

In our modules, microhabitat characteristics between the two spider genera were strongly differentiated: *Theridion* built webs in more concealed locations and on diverse substrates, whereas *Dictyna* built webs in more exposed locations and on a single substrate, which are situations known to enhance sensitivity to increased detrimental edge effects. As predicted by the nature of these microhabitat differences and how they link to edge sensitivity, spider species within the genus *Theridion* were able to take better advantage of the increased edge habitat offered by elongated patches compared to *Dictyna*, although the relative gain in preferred substrate on elongated modules was nearly the same for both genera. This pattern appears to originate from the structural properties of our modules, which created in our system a recurrent difference in microhabitat choice and in potential sensitivity across the two genera. The different responses of these ecologically similar genera to experimentally altered patch shape suggest a role of microhabitat choice on the outcome of habitat change on species abundances.

The unexpected lack of response of salticids and oxyopids to module shape may result from a preference for jute substrate, which was the thickest substrate and was available in the same amount in both module shapes. While we observed these families on both jute and wire, Ehmann (1994b) reported their preference for wider substrates, an inclination linked to improved mobility (Prenter et al. 2010). Nonetheless, there was one oxyopid or salticid for every two web spiders in the modules. Given the diversity of other
potential enemies that we observed at our site, including mantids, coleopterans, other spiders, and organisms that do not reside in modules (e.g. wasps and birds), web spiders in more concealed locations may have been less exposed to detrimental encounters, giving them an advantage in habitat patches that had more surface area, where species interactions at the edge were expected to be more frequent.

It seems unlikely that the response of *Theridion* and *Dictyna* to patch shape resulted from competitive encounters among one another for space or prey, because web counts and spider abundances revealed that modules contained appreciable amounts of unused substrate. In addition, predatory interactions between *Theridion* and *Dictyna* would have been minimal because web spiders are almost exclusively insectivorous (Nyffeler 1999). We also view the potential role of microclimatic differences between the two module shapes as unlikely, because modules had a simple, open architecture, and because module height, bottom surface area, and jute arrangement were identical, thereby minimizing environmental gradients.

Our results suggest that the different responses of web-spider abundance among habitat shapes were likely due to differences in microhabitat choice, a finding that is consistent with the idea that the biological characteristics of species are linked to their propensity to be sensitive to edges (Ries and Sisk 2010). Concealed microhabitats may buffer edge-dwelling species from the increased unfavorable interactions that can occur in complex habitat fragments. For instance, edge-dwelling organisms often suffer greater predation rates than organisms in the core of habitat patches (Ferguson 2000; Purger et al. 2004; Anderson and Burgin 2008). The choice of more concealed, structurally complex habitat to avoid detrimental encounters is prevalent among various taxa including spiders.
(Wise 2006; Manicom et al. 2008), insects (Atlegrim 1989), fish and lobsters (Eggleston et al. 1997) and birds (Jenks-Jay 1982), and can have important consequences at the population and community levels (Holbrook and Schmitt 2002).

A number of studies have also shown that habitat specialists are expected to suffer more strongly from habitat modification compared to habitat generalists (Henle et al. 2004). Since species traits can interact synergistically with each other to increase susceptibility to habitat fragmentation (Davies et al. 2004), it is likely that a microhabitat choice featuring greater exposure and substrate specialization in the modules made *Dictyna* susceptible to the detrimental effects of increased edge habitat. In contrast, substrate generalism in *Theridion* may have allowed the genus to build webs in a greater diversity of locations, thereby increasing the chances of finding suitable web sites and of augmenting its abundance. *Dictyna*’s specialization on wire may be linked to its predilection for thin, rigid substrates, which are typically found in the terminal parts of vegetation (Pearson 2009). The use of jute by *Theridion* may be explained by the presence of horizontal jute components under which webs could be built. Indeed, by changing the orientation of jute strands in wire modules similar to ours, Robinson (1981) found that *Theridion petraeum* preferred horizontal substrates. The different trends in abundance across our two spider genera are reminiscent of the patterns of species replacement described by Schmidt et al. (2008) and Herrmann et al. (2010) in spiders, and by Summerville (2004) in lepidopterans, in which specialist species are lost from habitat fragments while habitat generalists increase in abundance.

An alternative mechanism worth investigating is the possibility that *Theridion* gained benefits on elongated modules whereas *Dictyna* did not. For instance, module
shapes may have differed in the nature and amount of prey they attracted, whereby elongated modules offered better prey resources to *Theridion* compared to *Dictyna*. Specifically, given that *Theridion* used wire and jute as substrates, whereas *Dictyna* only used wire, *Theridion* may have benefited from a greater increase in prey on elongated modules compared to *Dictyna*, if for example jute represented a more attractive substrate for prey. *Theridion* and *Dictyna* do not differ much in their diet, which consists mainly of small insects such as dipterans, leafhoppers, aphids and small wasps (Nyffeler 1988; Pekar 2000). However, jute may represent a more attractive substrate for prey as its larger surface area can host more individuals compared to wire, and offer better protection from incident radiation and wind, which are factors known to influence arthropods in general (Cloudsley-Thompson 1962). Nevertheless, this benefit to increased edge in the form of enhanced prey availability would still support a role for microhabitat choice behind the observed response to increased edge habitat.

A caveat with respect to interpreting the data is that we did not pinpoint the specific mechanisms behind the response of the web spiders to module shape, as it would have been difficult to observe and interpret interactions involving these small organisms in the field without modifying and misinterpreting their behavior (Roberts et al. 2007). Further experiments in controlled environments may provide the opportunity to gain more insights into the immediate causes of our findings. In addition, research over larger spatiotemporal extents would help evaluate the constancy of patterns and the factors that may modify them, and would enable a better understanding of the effects that altered community structures may have on modified landscapes.
While habitat modification and its effects are typically documented at relatively large spatial scales (e.g. Ewers and Didham 2007), other studies demonstrate that small-scale architectural changes in individual plants and artificial habitat structures modify the composition of the spider communities within (Hatley and MacMahon 1980; Heikkinen and MacMahon 2004). Notable architectural attributes of microhabitat include substrate height, density, spatial arrangement, and diameter (Ehmann 1994b). A good understanding of these small-scale attributes on community composition should improve habitat management plans, because these traits shape the architecture of common and invasive plants, whose abundance or spread can fundamentally define the architectural characteristics of a habitat. For instance, Pearson (2009) found that *Dictyna* spiders significantly increased in abundance in response to the invasion of spotted knapweed, because this plant offered better web-building sites and enhanced foraging success compared to native vegetation. Such effects of plant architecture, which directly alter predator densities and behaviors, can substantially influence predator-prey interactions (Pearson 2009). Our study suggests that the surface area to volume ratio of small habitat patches is an attribute that may also play a role in shaping communities at larger spatial scales, especially in sedentary, edge-dwelling organisms such as web-building spiders.

Our study suggests trait-based community consequences to alterations of patch shape and supports microhabitat choice as a species-sorting mechanism in patches with increased edge habitat. The relatively rapid development of different spider assemblages on the modules, in which species showed different sensitivities to microhabitat and habitat patch shape, and the cost-effective sampling support studies that recommend spiders as adequate biological indicators of habitat modification (Pearce and Venier
2006; Buchholz 2010) via their potential to provide early warnings of environmental change. Since organisms that vary in their microhabitat requirements and that are affected by habitat modification and fragmentation include noxious species (Moksnes et al. 1998; Rand et al. 2006; Ewers and Didham 2007) and endangered species (Webb and Shine 1997; Hackett and Pagels 2003), predicting community structure accurately has important implications for the conservation and management of species and ecosystems.

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Table 4.1 Location and number of *Theridion* and *Dictyna* webs within cubic (C) and elongated (E) modules over the two combined observation periods. Web locations are listed in order of increasing concealment.

<table>
<thead>
<tr>
<th>Web location</th>
<th>Description</th>
<th>Substrate</th>
<th>Theridion</th>
<th>Dictyna</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>C  E</td>
<td>C  E</td>
</tr>
<tr>
<td>Face</td>
<td>Single side of the module</td>
<td>Wire</td>
<td>0  1</td>
<td>9  8</td>
</tr>
<tr>
<td>Ridge</td>
<td>Where two faces meet</td>
<td>Wire</td>
<td>7  28</td>
<td>8  8</td>
</tr>
<tr>
<td>Corner</td>
<td>Where three faces meet</td>
<td>Wire</td>
<td>5  9</td>
<td>4  2</td>
</tr>
<tr>
<td>Face + Jute</td>
<td>Module side and adjacent jute portion</td>
<td>Wire + jute</td>
<td>28 22</td>
<td>0  0</td>
</tr>
<tr>
<td>Ridge + Jute</td>
<td>Module ridge and adjacent jute portion</td>
<td>Wire + jute</td>
<td>15 39</td>
<td>0  0</td>
</tr>
</tbody>
</table>
Fig. 4.1 Difference in the amount of patch edge intercepted by a hypothetical isoline of visual discrimination acuity (circle) of a visual arthropod (black dot) in a cubic module compared to an elongated module of identical volume.
Fig. 4.2 Cubic and elongated modules. The outline of the chicken wire frame, jute strands and jute knots (where jute strands attach to chicken wire) are respectively represented by thin lines, thick lines and dots.
Fig. 4.3 Differences in concealment in Theridion and Dictyna. a. Immature Theridion sp. between 2 wires inside a plastic cable tie; b. Theridion petraeum under a jute knot (jute fibers on the left are lifted to better reveal the spider and web); c. Dictyna idahoana exposed on chicken wire; d. “flat” Dictyna web on chicken wire.
Fig. 4.4 Family-level box plots of total spider abundance on cubic modules and elongated modules (ADONIS, $F = 5.420$, $R^2 = 0.124$, $P = 0.028$). Medians are indicated by the horizontal bar, the extent of the boxes indicates 25th and 75th percentiles; the extent of the whiskers indicates 10th and 90th percentiles, and dots represent 5th and 95th percentiles. Theridiids were significantly more abundant on elongated modules than on cubic modules (Wilcoxon rank-sum test, $Z = -2.741$, $P = 0.006$).
CHAPTER 5

CONCLUSIONS

Spatial patterns of community structure are well documented, but there is no consensus for the exact mechanisms underlying them (Gaston 2000; Lessard et al. 2011). It is essential that we improve our understanding of the drivers of biological diversity, because the effects of habitat modification and climate change are expected to intensify in the near future, with large numbers of species becoming endangered (Thomas et al. 2004). The aim of this thesis was to focus on spider assemblages to investigate how the fine-scale habitat associations of organisms may drive their community composition at bigger scales.

Patterns of diversity along elevational gradients are notoriously challenging to explain (McCoy 1990; Lessard et al. 2011). In Chapter 1, I hypothesized that the omission of small-scale, topographically-induced site characteristics such as microclimate and vegetation structure may be a source of inconsistent findings across studies. I studied spider communities in the Bear River Mountains to determine if sites on different slope aspects at a given elevation could contain different spider communities, and to assess if the drivers of spatial variation in community structure differed among spider guilds. I found that slope aspect was a significant predictor of spider density and species richness, and that differences in cursorial spider composition were strongly driven by temperature dissimilarity only, whereas differences across web spider assemblages significantly increased with dissimilarities in woody plant cover and temperature. These results suggest that fine-scale topographic variables play an important role in shaping
elevational patterns of species composition, and that a better understanding of the links between the biological traits of species and their environmental requirements should help uncover the mechanisms behind topographic patterns of diversity.

In Chapter 3, I built on studies that have quantified the role of species mobility in predicting sensitivity to adjacent habitat structure in already-existing landscapes (e.g. Weibull and Ostman 2003; Dauber et al. 2005; Cole et al. 2010), by running a small-scale manipulative field experiment subject to fewer confounding variables. I collected spiders of contrasting mobility to investigate the effects of neighboring habitat structure on their community composition, and found that guild and community differences across treatments were strongly driven by cursorial spiders. In particular, there were markedly reduced cursorial spider densities in shrubs without surrounding structure, and more cursorial species in control shrubs, whereas web spiders lacked any significant response to treatments. The contrasting responses of the two spider guilds suggest that mobility may mediate the outcome of surrounding habitat modifications on the local composition of spider communities, and may be a predictor of sensitivity to ecological processes that act at larger spatial scales. Based on these results, it is recommended that data be collected at larger spatial extents for mobile species to avoid missing important information on their habitat associations. More generally, approaches to collecting species habitat data should improve if we recognize the role of biological traits in shaping the composition of communities.

In Chapter 4, I investigated the potential for the microhabitat preference of organisms to predict their sensitivity to habitat fragmentation. Increased habitat edge, one of the most important consequences of habitat fragmentation, is an ecologically important
factor because the abundance of edge-dwelling species should increase with habitat shape complexity (Ewers and Didham 2007). I ran a field experiment with artificial shrub modules (habitat patches) of specific size, structure and shape to investigate how microhabitat choice, a species characteristic that reflects combinations of biological traits, may affect the ability of web-building spider species that live at the periphery of habitat patches to take advantage of increases in edge habitat. I found that the tangle-web spiders *Theridion* and *Dictyna* built webs on module edges and strongly differed in terms of concealment and substrate generalization, two habitat characteristics associated with lower vulnerability to habitat modification. *Theridion* built webs in more concealed locations and on a greater diversity of substrate configurations in the modules compared to *Dictyna*. As predicted by the nature of these microhabitat differences and how they link to edge sensitivity, *Theridion* was significantly more abundant on elongated modules whereas the abundance of *Dictyna* did not respond to shape, even though the change in module shape entailed a similar increase in favored substrate for both spider groups. The different responses of these ecologically similar genera to experimentally altered patch shape suggest a role of microhabitat choice on the outcome of habitat geometry on species abundances. This study highlights that a better understanding of the effects of small-scale habitat attributes on community composition should improve habitat management plans. For instance, microhabitat attributes shape the architecture of common and invasive plants, whose abundance or spread can fundamentally define the architectural characteristics of habitats at larger scales (e.g. Pearson 2009), and generate cascading effects on the density and behavior of predators and prey.
The studies presented here focused on the biological and environmental factors that may drive spider distribution patterns, but additional work is needed to identify the immediate causes of our findings. For instance, it would be insightful to determine why temperature was a much stronger correlate of spider community composition in cursorial spiders than in web spiders (Chapter 2). This knowledge would enable more specific predictions and hypotheses to be tested in spiders and in other organisms that differ in mobility. Similarly, I did not pinpoint the specific mechanisms behind the response of web spiders to shrub module shape (Chapter 4), due to the difficulty of observing the interactions of small organisms in the field (Roberts et al. 2007). Further experiments in controlled environments may provide the opportunity to gain more insights into the direct mechanisms behind our results.

In conclusion, this research provides evidence for the role of fine-scale habitat associations in shaping patterns of community composition at larger scales, and reveals biological characteristics that may be associated with some of the mechanisms behind species diversity gradients. While my dissertation focused on spiders specifically, these findings may help improve the study and management of other organisms, especially small-bodied species, which are often studied at much greater spatial resolutions than those at which they perceive their environment.

References


APPENDIX
Table A.1 List of spiders collected in big sagebrush shrubs in Logan Canyon, Utah.

<table>
<thead>
<tr>
<th>Guild</th>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cursorial</td>
<td>Anyphaenidae</td>
<td><em>Anyphaena</em></td>
<td><em>pacific</em> (Banks 1896)</td>
</tr>
<tr>
<td></td>
<td>Corinnidae</td>
<td><em>Castianeira</em></td>
<td><em>sp.</em></td>
</tr>
<tr>
<td></td>
<td>Gnaphosidae</td>
<td><em>Drassodes</em></td>
<td><em>saccatus</em> (Emerton 1890)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Drassylus</em></td>
<td><em>sp.</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Gnaphosa</em></td>
<td><em>sericata</em> (L. Koch 1866)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Micaria</em></td>
<td><em>sp.</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Sergiolus</em></td>
<td><em>montanus</em> (Emerton 1890)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Zelotes</em></td>
<td><em>fratris</em> Chamberlin 1920</td>
</tr>
<tr>
<td></td>
<td>Lycosidae</td>
<td><em>Alopecosa</em></td>
<td><em>sp.</em></td>
</tr>
<tr>
<td></td>
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<td><em>Pardosa</em></td>
<td><em>utahensis</em> Chamberlin 1919</td>
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<td><em>wyuta</em> Gertsch 1934</td>
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<td><em>Schizocosa</em></td>
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<td>Mimetidae</td>
<td><em>Mimetus</em></td>
<td><em>aktius</em> Chamberlin &amp; Ivie 1935</td>
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<td>Oxyopidae</td>
<td><em>Oxyopes</em></td>
<td><em>scalaris</em> Hentz 1845</td>
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<td>Philodromidae</td>
<td><em>Ebo</em></td>
<td><em>pepinensis</em> Gertsch 1933</td>
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<td><em>Philodromus</em></td>
<td><em>californicus</em> Keyserling 1884</td>
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<td><em>histrio</em> (Latreille 1819)</td>
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<td><em>marxi</em> Keyserling 1884</td>
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<td><em>rufus</em> Walckenaer 1826</td>
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<td><em>Thanatus</em></td>
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<td><em>Tibellus</em></td>
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<td>Salticidae</td>
<td><em>Dendryphantes</em></td>
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<td><em>hoyi</em> (Peckham &amp; Peckham 1883)</td>
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<td><em>Habronattus</em></td>
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<td><em>hirsutus</em> (Peckham &amp; Peckham 1888)</td>
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<td>Misumena vatia (Clerck 1757)</td>
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<td>Xysticus cunctator Thorell 1877</td>
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<td>Gulosus Keyserling 1880</td>
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<td>Montanensis Keyserling 1887</td>
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<td>Web-builder</td>
<td>Aculepeira packardi (Thorell 1875)</td>
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<td>Araneus gemmoides Chamberlin &amp; Ivie 1935</td>
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<td>Araniella duplicata (Hentz 1847)</td>
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<td>Cyclosa conica (Pallas 1772)</td>
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<td>Hypsosinga sp.</td>
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<td>Metepeira foxi Gertsch &amp; Ivie 1936</td>
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<td>Dictyna idahoana Chamberlin &amp; Ivie 1933</td>
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<td>Emblyna piratica (Ivie 1947)</td>
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<td>Reticulata (Gertsch &amp; Ivie 1936)</td>
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<td>Erigone dentosa O. P.-Cambridge 1894</td>
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<td>Frontinella communis (Hentz 1850)</td>
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<td>Meioneta sp.</td>
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<td>Psilochorus sp.</td>
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<td>Tetragnatha laboriosa Hentz 1850</td>
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<td>Theridiidae</td>
<td>Chrysso nordica (Chamberlin &amp; Ivie 1947)</td>
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<td>Pelyx (Levi 1947)</td>
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<td>Dipoena nigra (Emerton 1882)</td>
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<td>Euryopis sp.</td>
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<td><em>Latrodectus</em></td>
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<td><em>neomexicanum</em></td>
<td>Banks 1901</td>
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<td>L. Koch 1872</td>
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| **DOI**          | **Corresponding Author**                        |
| 10.1007/s10841-011-9443-2 | Stephanie Cobbold |
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CURRICULUM VITAE

STEPHANIE M. COBBOLD

(April 2012)

EDUCATION

**PhD candidate, Biology-Ecology.** 2006-present. Utah State University, Logan, Utah. Advisor: Dr. James A. MacMahon.

The role of fine-scale habitat associations in structuring spider assemblages: determinants of spatial patterns in community composition.


Comparative analysis of an adaptive radiation: origins of the variation in vulnerability to extinction risk among Hawaiian honeycreepers.


Licence Biologie des Organismes, Université de Rennes 1, France (Mention Bien). 2002-2003.


RESEARCH EXPERIENCE

**Laboratory assistant.** 2004. Utah State University (Dr. M.E. Pfrender).

Life history responses to predation pressure and the genetic mechanisms of UV resistance in Daphnia, in high-alpine lakes of the Sierra Nevada. Six months, undergraduate research.

Development of genetic markers for Pine Beetles (*Ips sp.*).
**Field assistant.** 2004. Utah State University.

Home range, movement patterns, and habitat use in willow flycatchers (*Empidonax traillii*). Fish Creek, Utah.

**Field assistant.** 2002. Université de Rennes 1, France (Dr. A. Guéguen).

Biological cycles and adaptations of two species of cricket to their environment in Mercantour National Park, French Alps.

**Field and laboratory assistant.** 2002. Université de Rennes 1, France.

Consequences of the spreading of *Elytrigia sp.* on the distribution of spider populations in the Bay of Mont Saint Michel, France.

**Field assistant.** 2000. CIES research centre, Iguazu National Park, Argentina

Behavior of *Cebus apella*, and the possibility of their social status being transferred from one generation to another (Dr. M. Dibitetti).

Conservation and management of jaguars (*Panthera onca*), inside and around Iguazu National Park (Dr. K. Schiaffino).

**PEER-REVIEWED PUBLICATIONS**


RESEARCH TECHNIQUES

- Field sampling of insects, spiders, and small mammals.
- Identification of insects, spiders, and birds.
- Collection of behavioral data
- Computer programs: ArcGIS, statistical computing in R, PAST (PAleontological STatistics), and SAM (Spatial Analysis in Macroecology).
- Molecular laboratory techniques: DNA and RNA extraction, PCR amplification, electrophoresis.
- Laboratory culture maintenance, life history trait measurements (Daphnia).

PROFESSIONAL PRESENTATIONS


GRANTS & ASSISTANTSHIPS
Ecology Center PhD Assistantship. 2010-2011. Utah State University. $12000.

Ecology Center Graduate Research Support Award. 2010-2011. Utah State University. $4000.

Ecology Center Graduate Research Support Award. 2008-2009. Utah State University. $4500.


TEACHING EXPERIENCE AND OUTREACH


Teaching assistant. 2010. Ornithology. Utah State University.


Team arachnologist, Antelope Island Bioblitz. 2009. Utah.

Interviewer for the Utah State University NSF ADVANCE program. 2007. 92nd Annual Meeting of the Ecological Society.

Member, CNER (Cercle Naturaliste des Etudiants Rennais). 2002-2003. Université de Rennes 1, France


OTHER SKILLS

Fluent in English, French, and Spanish.

Certified open water scuba diver (PADI)