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Causes and Consequences of Plant Spatial Patterns on Natural and Experimental Great Basin (USA) Plant Communities

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CAUSES AND CONSEQUENCES OF PLANT SPATIAL PATTERNS IN NATURAL

AND EXPERIMENTAL GREAT BASIN PLANT COMMUNITIES

by

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ABSTRACT

Causes and Consequences of Plant Spatial Patterns on Natural and

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by

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Utah State University, 2011

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The processes by which plant spatial patterns are formed, and the effects of those

patterns on plant community dynamics, remain important areas of research in plant

ecology. Plant spatial pattern formation has been linked to many ecological processes

that act to structure plant communities at different spatiotemporal scales. Past studies of

pattern formation are common, but recent methodological advances in data collection and

analysis have permitted researchers to conduct more advanced observational studies of

pattern formation in space and time. While studies of the effects of plant spatial patterns

were formally rare, they have increased in the last decade as new types of experiments

and analysis have been developed to better understand the myriad effects of plant patterns

on community dynamics. My dissertation research examined both the causes and

consequences of plant spatial patterns in the context of natural and experimental Great

Basin semi-arid plant communities. In both cases, I implemented novel methodologies

for data collection, experimental design, and data analysis in an attempt to address

current gaps in knowledge related to the processes by which plant spatial patterns are

formed, as well as the effect of plant spatial patterns on community dynamics. The results

inform both basic and applied plant ecology, and set the stage for further research on the

causes and consequences of plant spatial patterns in semi-arid plant communities.

(161 pages)

PUBLIC ABSTRACT

Causes and Consequences of Plant Spatial Patterns on Natural and

Experimental Great Basin (USA) Plant Communities

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There are many ways to describe plant communities and the different plant

species of which they are comprised. One approach is to study the spatial patterns of

plants; that is, the physical arrangement or distribution of plants within the community.

Plant spatial patterns are often described in terms of the two-dimensional location of

individual plants (e.g., latitude and longitude), analogous to the (x,y) coordinates of the

Cartesian grid. Plant patterns result from important ecological processes that structure

plant communities, including competition between plants for limited resources like water

and light, the effects of fire and other forms of disturbance, and the response of plants to

being eaten by livestock and other herbivores.

From 2006-2011, in pursuit of my Ph.D. at Utah State University, I conducted

four relatively inexpensive field experiments to study both the causes and consequences

of plant spatial patterns in semi-arid shrub communities in the Great Basin region of the

western United States. These experiments were performed with the help of many

different collaborators, ranging from undergraduate technicians, fellow graduate students,

federal scientists, and professors from national and international institutions. These

experiments were both observational and manipulative in nature; for three of the

experiments, I and my collaborators collected and analyzed observational data on natural

plant communities, while the fourth experiment involved the construction and

measurement of artificial plant communities designed to test the effects of different plant

spatial patterns. These experiments were designed to address important questions in the

field of plant ecology, based on my review of the existing scientific literature in 2006.

In the course of my research, I and my collaborators were able to develop and/or

implement novel methodologies for data collection and analysis that we anticipate will be

used in the future by other researchers. Two dissertation chapters have already been

accepted for publication in the peer-reviewed literature, and we anticipate that the

remaining chapters will be published soon. Our results inform both basic and applied

plant ecology, and set the stage for future research on the causes and consequences of

plant spatial patterns.

ACKNOWLEDGMENTS

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CHAPTER I

INTRODUCTION

The spatial patterns of plants in natural plant communities are rarely random; instead, plants are often spaced closer or farther away from one another than would be expected by chance (Stoll & Prati 2001; Maestre *et al*. 2005; Rayburn *et al*. 2011). The causes and consequences of these patterns remain important topics in plant ecology (Raventós *et al*. 2010).

The processes that generate plant spatial patterns in natural communities include plant-plant interactions (Phillips & MacMahon 1981; Skarpe 1991; Valiente-Banuet *et al*. 2006), environmental heterogeneity (Schenk *et al*. 2003; Perry *et al.* 2009), seed dispersal (Schurr *et al*. 2004), and disturbance (Rebollo *et al*. 2002; Bisigato *et al*. 2005; Rayburn & Monaco 2011).

There is an extensive history of observational research that has sought to explain the formation of plant spatial patterns by connecting observed patterns to ecological processes. Observational pattern studies have tended to involve the collection of some form of spatial data on the pattern(s) of one or more species within a community, followed by statistical analysis that seeks to describe the patterns of the plants of interest. Results are then linked to the ecological process(es) by which the patterns are hypothesized to have formed. Oftentimes, observed patterns have been linked to either positive or negative plant interactions that have the potential to structure local plant neighborhoods (Phillips & MacMahon 1981, Valiente-Banuet & Verdú 2006; Rayburn & Monaco 2011). For example, regular plant spatial patterns are often interpreted as a sign

of intense competition between plants for limited resources (Kenkel 1998; Stoll &
Bergius 2005; Rayburn & Monaco 2011). In contrast, more aggregated patterns
(especially interspecific aggregations) are interpreted as evidence of neutral or positive
plant interactions (Eccles *et al*. 1999; Kéfi *et al*. 2007; Valiente-Banuet & Verdú 2008).
Aggregated plant patterns have also been linked to patchy distributions of soil resources,
especially in shrub-dominated communities (Schenk *et al*. 2003; Tirado & Pugnaire
2003; Perry *et al*. 2008; Perry *et al*. 2009). Disturbance via grazing is also recognized as
playing a significant role in spatial pattern formation (Adler *et al*. 2001; Seifan &
Kadmon 2006, Rayburn & Monaco 2011). Depending on the framework of the study,
observational studies of plant spatial patterns may be able to differentiate the effects of
multiple processes on pattern formation (Fajardo & McIntire 2007; Rayburn & Monaco
2011). For example, Rayburn & Monaco (2011) used a combination of precise spatial
data and *a priori* hypotheses to approximately separate the effects of intraspecific
competition and grazing on pattern formation along a chronosequence of grazed Great
Basin grasslands. Past observational studies have utilized various methods of data
collection (Phillips & MacMahon 1981, Boose *et al*. 1998; Schurr *et al*. 2004), however
these techniques were often time-consuming in the field, as well as being prone to
significant measurement error that could bias statistical analysis (Freeman & Ford 2002;
Rayburn *et al*. 2011). With the advent of new methodologies in recent years for
experimental design (Fajardo & McIntire 2007; Rayburn & Monaco 2011), data
collection (Strand *et al*. 2006; Rayburn *et al*. 2011) and analysis (Wiegand & Moloney
2004; Wiegand *et al*. 2007; Schiffers *et al*. 2008; Raventós *et al*. 2010), the power of

observational studies of plant spatial patterns to link observed patterns to ecological processes has grown.

While studies of the causes of plant spatial patterns are common, studies of the consequences of plant spatial patterns are relatively rare (Tilman & Kareiva 1997; Murrell &. 2001; Stoll & Prati 2001; Maestre *et al*. 2005; Turnbull *et al*. 2007). Rarer still are empirical field studies in which the actual patterns of plants are manipulated in order to test for the effects of plant patterns on community dynamics and/or species coexistence (Turnbull *et al*. 2007). Numerous theoretical studies have modeled the effects of spatial structure on plant populations and communities (Czárán & Bartha 1992; Silvertown *et al*. 1992; Pacala & Deutschman 1995; Bolker *et al*. 2003; De Boeck *et al*. 2006; Turnbull *et al*. 2007). For example, Silvertown *et al*. (1992) used a cellular automaton model to simulate the effect of different spatial arrangements on the competitive interactions between grass species, and concluded that spatial pattern may have a profound effect on determining the outcome of interspecific competition. More recently, De Boeck *et al*. (2006) examined the effect of spatial aggregation of plants on below-ground resource uptake, while Turnbull *et al*. (2007) used field-parameterized neighborhood models to examine the effects of spatial structure on the dynamics of annual plant communities. These and other theoretical studies have conclusively demonstrated that plant spatial patterns may have substantial impacts on population and community dynamics, but that relationships between plant patterns and ecological processes may be complex and depend crucially on the details associated with realistic communities (Turnbull *et al*. 2007).

Similar results have been obtained from observational studies of the effects of plant spatial patterns, which have tended to focus on the effects of pattern on plant interactions. Tirado & Pugnaire (2003) examined the spatial distribution of two semi-arid shrubs to test if aggregation of the smaller shrub in patches of the larger shrub was a consequence of a positive interaction between the two species. The results suggested that transplanted individuals of the smaller shrub species had high survival rates, more fruits and flowers, and higher seed mass in patches versus in the open. Hegazy *et al.* (2005) looked at spatial patterns in relation to alleopathy, finding that the degree of clustering of a desert annual affected its alleopathic potential on surrounding annual and perennial desert plants.

Once rare, empirical tests of the effects of plant spatial patterns are becoming more common. Schmid & Harper (1985) found that regular versus aggregated planting patterns had little to no influence on the competitive relationship between two species of perennial grasses with different growth forms. Bergelson (1990) found that the spatial distribution of an annual grass dramatically influenced the per capita seedling production of interspecific competitors. Tyler & D'Antonio (1995) showed that both survivorship and growth of shrub seedlings increased with increasing distance from near neighbors, while MacMahon (1997) discussed how clustered plantings of shrubby vegetation on mine reclamation sites led to increased growth and more successful establishment. More recent studies have generally focused on the testing the effects of intraspecific aggregation on species interactions and coexistence (Stoll & Prati 2001; Monzeglio & Stoll 2005; Mokany *et al.* 2008; Lamošová *et al.* 2010). These studies have presented convincing evidence that intraspecific aggregations may benefit weaker competitors by

reducing the frequency of interspecific interactions and potentially slowing competitive

exclusion (Stoll & Prati 2001; Monzeglio & Stoll 2005; Mokany *et al*. 2008). For

example, Stoll & Prati (2001) and Monzeglio & Stoll (2005) found that the spatial

distribution of individual plants significantly affected the competitive environment within

artificial plant communities, such that weaker competitors increased their fitness while

stronger competitors were suppressed when grown in neighborhoods of conspecifics. The

general conclusion that has emerged from empirical tests of the effects of plant spatial

patterns, that plant spatial patterns may significantly affect both community and

population dynamics, reinforces the findings of past theoretical and observational

research. Questions remain, however, as to effects of plant spatial patterns in realistic

communities since past experiments have focused on only annual vegetation over short

temporal scales (e.g. Stoll & Prati 2001; Monzeglio & Stoll 2005; Turnbull *et al*. 2007).

There is also still substantial uncertainty as to the effects of plant spatial patterns

on other aspects of community dynamics, such as the distribution of abiotic plant

resources, such as soil moisture (Bhark & Small 2003; Cantón *et al*. 2004), and light

(Martens *et al*. 2000; Valladares 2003; Mokany *et al*. 2008). The pattern of above-ground

vegetation may be a crucial determinant of the distribution of light and soil moisture

(Martens *et al*. 2000; Valladares 2003; Cantón *et al*. 2004) that in turn may critically

affect both community and population dynamics (Harper 1997; Valladares 2003; Armas

& Pugnaire 2005), yet few studies have manipulated plant spatial patterns in order to test

the effect of different patterns on resource distribution (Bolker *et al*. 2003). One

exception is the study by Martens *et al*. (2000) that tested the effects of canopy spatial

pattern on the distribution of understory light along a grassland-forest gradient. In many

communities, such as semi-arid grasslands, much remains unknown as to how different vegetation patterns affect the distribution of plant resources.

The studies that comprise my Ph.D. dissertation address both the causes (data chapters 2-4) and the consequences (data chapter 5) of plant spatial patterns in the context of natural and experimental semi-arid Great Basin (USA) plant communities. The studies were designed to test novel methodologies for experimental design, data collection, and data analysis, and address current gaps in knowledge related to both spatial pattern formation and the effects of plant spatial patterns on community dynamics.

In the first data chapter, published in 2011 in the journal *Plant Ecology*, my co-authors and I developed a GPS-based methodology for the rapid collection of precise spatial data on species and location of 2358 shrubs in a semi-arid Great Basin shrubland. We used recently-developed univariate and bivariate spatial statistics to test for aggregation within the shrub community and found strong statistical evidence of fine-scale aggregation (1) independent of species, (2) within species, and (3) between two species pairs. Our approach will be useful for rapidly collecting precise spatial data in plant communities, and has various applications related to research, management and conservation.

In the next chapter, my co-author and I reanalyzed the shrub spatial data from the first chapter using a novel set of statistical methodologies designed to investigate spatial patterns of species diversity. We found significant fine-scale variation in diversity patterns, suggesting that two of the five shrub species had subtle effects on local neighborhood diversity within the well-mixed shrub community. Our approach may be used in other communities to describe multispecies spatial patterns, to quantify species-

specific effects on diversity patterns, and to link patterns to community-structuring processes.

In the third chapter, published in 2011 in the journal *Rangeland Ecology and Management*, my co-author and I used a novel approach to test for the effects of intraspecific competition and grazing on pattern formation along a chronosequence of grazed semi-arid Great Basin grass communities. Similar to methodologies presented in the first data chapter, we used a survey-grade GPS to quantify grass spatial patterns in stands that differed only in time since planting (9 – 57 yrs), as well as in a 57 yr old grazing exclosure to examine pattern formation in the absence of grazing. We detected fine-scale regularity, likely a sign of interference via resource competition, in all stands including the exclosure. Broader-scale aggregation, which we attributed to the effects of prolonged grazing disturbance, was only detected in the oldest grazed stand. Our results suggested that competition acts over finer spatial and temporal scales than grazing in structuring these stands, and reinforced the importance of both processes in structuring semi-arid communities.

In the final data chapter, I report the results of a unique multi-year field experiment conducted by myself and my co-author in which we tested the effects of community-scale plant spatial patterns and fine-scale aggregation on both biotic (above-ground biomass and relative growth rate) and abiotic components (heterogeneity of light and soil moisture) of experimental semi-arid grassland communities comprised of a strongly competitive introduced bunchgrass and a relatively weaker native Great Basin bunchgrass. We found that spatial treatments had profound effects on biomass production and relative growth rates of both species, but were different for each species and likely

linked to each species' competitive ability. Treatments also affected the heterogeneity of light and soil moisture, and the effects of treatment on both biotic and abiotic aspects of community dynamics were generally different across years.

References

Adler, P. B., Raff, D. A. & Laurenroth, W. K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465-479.

Armas, C. & Pugnaire, F. I. 2005. Plant interactions govern population dynamics in a semi-arid plant community. J. Ecol. 93:978-989.

Bergelson, J. 1990. Life after death: site pre-emption by the remains of *Poa annua*. Ecol. 71:2157-2165.

Bhark, E. W. & Small, E. E. 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems 6:185-19.6

Bisigato, A. J., Bertiller, M.B., Ares, J. O. & Pazos, G. E. 2005. Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. Ecography 28:561-572.

Bolker, B. M., Pacala, S. W. & Neuhauser, C. 2003. Spatial dynamics in model plant communities: what do we really know? Amer. Nat. 162:135-148.

Boose, E. R., Boose, E. F. & Lezberg, A. L. 1998. A practical method for mapping trees using distance measurements. Ecol. 79:819-827.

Cantón, Y., Solé-Benet, A. & Domingo, F. 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. J. Hydrol 285:199-214.

Czárán, T. & Bartha, S. 1992. Spatiotemporal dynamic models of plant populations and communities. Trends Ecol. Evol. 7:38-42.

De Boeck, H. J., Nijs, I., Lemmens, C. M. H. M. & Ceulemans, R. 2006. Underlying effects of spatial aggregation (clumping) in relationships between plant diversity and resource uptake. Oikos 113:269-278.

Eccles, N. S., Esler, K. J. & Cowling, R. M. 1999. Spatial pattern analysis in Namaqualand desert plant communities: evidence for general positive interactions. Plant Ecol. 142:71-85.

Fajardo, A. & McIntire, E. J. B. 2007. Distinguishing microsite and competition processes in tree growth dynamics: an a priori spatial modeling approach. Amer. Nat. 165:647-661.

Freeman, E. A. & Ford, E. D. 2002. Effects of data quality on analysis of ecological pattern using the K(d) statistical function. Ecol. 83(1):35-46.

Harper, J. L. 1997. Population biology of plants. Academic Press, London.

Hegazy, A. K., Elfiky, A. & Kabiel, H. F. 2005. Spatial pattern and mulching effect of *Anastatica hierochuntica* L. on structure and function of some desert plants. In: Harper, J. D. I *et al*. (eds), Proceedings of the 4th World Congress on Allelopathy, Charles Sturt University, Wagga Wagga, NSW, Australia., pp 21-26.

Kéfi S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A. & de Ruiter, P. C. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213-217.

Kenkel, N. C. 1988. Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. Ecol. 69:1017-1024.

Lamošová, T., Doležal, J., Lanta, V. & Leps, J. 2010. Spatial pattern affects diversity-productivity relationships in experimental meadow communities. Acta Oecol. 36:325-332.

MacMahon, J. A. 1997. Ecological restoration. In: Meffe, G. K. *et al.* (eds), Principles of conservation biology, Sinauer Associates, Inc., Sunderland, pp 479-511.

Maestre, F. T., Escudero, A., Martinez, I., Guerreros, C. & Rubio, A. 2005. Does spatial pattern matter to ecosystem functioning? Insights from biological soil crusts. Funct. Ecol. 19:566-573.

Martens, S. N., Breshears, D. D. & Meyer, C.W. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecol. Model. 126:79-93.

Mokany, K., Ash, J. & Roxburgh, S. 2008. Effects of spatial aggregation on competition, complementarity, and resource use. Austral Ecol. 33:261-270.

Monzeglio, U. & Stoll, P. 2005. Spatial patterns and species performance in experimental plant communities. Oecologia 145:619-628.

Murrell, D. J., Purves, D. W. & Law, R. 2001. Uniting pattern and process in plant ecology. Trends Ecol. Evol. 16:529-530.

Pacala, S. W. & Deutschman, D. H. 1995. Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. Oikos 74:357-365.

Perry, G. L. W., Enright, N. J., Miller, B. P. & Lamont, B.B. 2008. Spatial patterns in species-rich sclerophyll shrublands of southwestern Australia. J. Veg. Sci. 19:705-716.

Perry, G. L. W., Enright, N. J., Miller, B. P. & Lamont, B. B. 2009. Nearest-neighbor interactions in species-rich shrublands: the roles of abundance, spatial patterns and resources. Oikos 118:161-174.

Phillips, D. L. & MacMahon, J. A. 1981. Competition and spacing patterns in desert shrubs. J. Ecol. 69:97-115.

Rayburn, A. P., Schiffers, K. J. & Schupp, E. A. 2011. Use of precise spatial data for describing spatial patterns and plant interactions in a diverse Great Basin shrub community. Plant Ecol. 212:585-594.

Rayburn, A. P. & Monaco, T. A. 2011. Using a chronosequence to link plant spatial patterns and ecological processes in grazed Great Basin plant communities. Rangeland Ecol. Manag. 64:276-282.

Raventós, J., Wiegand, T. & De Luis, M. 2010. Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland. Ecol. 91:2110-2120.

Rebollo, S., Milchunas, D. G., Noy-Meir, I. & Chapman, P. L. 2002. The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. Oikos 98:53-64.

Schenk, H. J., Holzapfel, C., Hamilton, J. G. & Mahall, B. E. 2003. Spatial ecology of a small desert shrub on adjacent geological substrates. J. Ecol. 91:383-395.

Schiffers, K., Schurr, F. M., Tielbörger, K., Urbach, C., Moloney, K., & Jeltsch, F. 2008. Dealing with virtual aggregation – a new index for analyzing heterogeneous point patterns. Ecography 31:545-555.

Schmid, B. & Harper, J. L. 1985. Clonal growth in grassland perennials. I. Density and pattern-dependent competition between plants with different growth forms. J. Ecol. 73:793-808.

Schurr, F. M., Bossdorf, O., Milton, S. J. & Schumacher, J. 2004. Spatial pattern formation in semi-arid shrubland: a priori predicted versus observed pattern characteristics. Plant Ecol. 173:271-282.

Seifan, M. & Kadmon, R. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a Mediterranean scrub community. Basic and Applied Ecol. 7:496-506.

Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. J. Veg. Sci. 2:565-572.

Silvertown, J., Holtier, S., Johnson, J. & Dale, P. 1992. Cellular automaton models of interspecific competition for space – the effect of pattern on process. J. Ecol. 80:527-534.

Stoll, P. & Prati, D. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. Ecol. 82:319-327.

Stoll, P. & Bergius, E. 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. J. Ecol. 93:395-403.

Strand, E. K., Vierling, L. A., Smith, A. M., Bunting, S. C., Hann, D. B. & Gessler, P. E. 2006. Wavelet estimation of plant spatial patterns in multitemporal aerial photography. Int. J. Remote Sens. 27:2049-2054.

Tilman, D. & Kareiva, P. 1997. The role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, NJ.

Tirado, R. & Pugnaire, F. I. 2003. Shrub spatial aggregation and consequences for
 reproductive success. Oecologia 136:296-301.

Turnbull, L. A., Coomes, D. A., Purves, D. W. & Rees, M. 2007. How spatial structure
 alters population and community dynamics in a natural plant community. J. Ecol.
 95:79-89.

Tyler, C. M. & D'Antonio, C. M. 1995. The effects of neighbors on the growth and
 survivorship of shrub seedlings following fire. Oecologia 102:255-264.

Valiente-Banuet, A., Verdú, M. & Callaway, R. M. 2006. Modern Quaternary plant
 lineages promote diversity through facilitation of ancient Tertiary lineages. Proc.
 Natl. Acad. Sci. 103:16812-16817.

Valiente-Banuet, A. & Verdú, M. 2008. Temporal shifts from facilitation to competition
 occur between closely related taxa. J. Ecol. 96:489-494.

Valladares, F. 2003. Light heterogeneity and plants: from ecophysiology to species
 coexistence and biodiversity. Prog. Bot. 64:439-471.

Wiegand, T. & Moloney, K. A. 2004. Rings, circles, and null-models for point pattern
 analysis in ecology. Oikos 104:209-229.

Wiegand, T., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N. & Okuda, T. 2007. Analyzing
 the spatial structure of a Sri Lankan tree species with multiple scales of clustering.
 Ecol. 88:3088–3102.

CHAPTER II

USE OF PRECISE SPATIAL DATA FOR DESCRIBING SPATIAL

PATTERNS AND PLANT INTERACTIONS IN A DIVERSE

GREAT BASIN SHRUB COMMUNITY[1] [2]

Abstract

Community-structuring processes continue to be of great interest to plant

ecologists, and plant spatial patterns have been linked to processes including disturbance,

dispersal, environmental heterogeneity, and plant interactions. Under the assumption that

the analysis of the spatial structure of plant communities can help to elucidate the type

and importance of the predominant community-structuring processes, many studies have

analyzed point pattern data on various plant species. A variety of methods have been

devised to acquire point pattern data for individual plants, however the classic tradeoff

between the speed of acquisition and the precision of spatial data has meant that large and

precise datasets on plant locations are difficult to obtain.

The primary goal of this study was to develop a GPS-based methodology for the

rapid collection of precise spatial data on plant locations in a semi-arid shrubland in the

Great Basin, USA. The secondary goal was to demonstrate a potential application of this

approach by using recently developed univariate and bivariate spatial statistics to test for

aggregation within the shrub community, as observed in other semi-arid shrublands. We

efficiently mapped 2358 individuals of five shrub species with a spatial error of ≤ 0.02 m,

and found strong statistical evidence of fine-scale aggregation (1) independent of species, (2) within species, and (3) between two species pairs. Our approach is useful for rapidly collecting precise point pattern data in plant communities, and has other applications related to population modeling, GIS analysis, and conservation.

Introduction

Processes that structure plant communities continue to be a primary focus of plant ecological research (Stoll & Prati 2001; Armas & Pugnaire 2005; Mokany *et al*. 2008). For example, the role of plant-plant interactions in structuring communities and affecting species coexistence remains uncertain despite extensive experimental and theoretical research. This is especially true for arid and semi-arid plant communities where debate over the existence, direction, and magnitude of interactions persist (Phillips & MacMahon 1981; Fowler 1986; Armas & Pugnaire 2005; Brooker *et al*. 2008; Mokany *et al*. 2008).

Theoretical models have demonstrated that the spatial structure of plant communities may influence a wide variety of ecological processes, such as intra- and interspecific competition between plants (Phillips & MacMahon 1981; Tielbörger & Kadmon 2000; Schenk *et al*. 2003; Tirado & Pugnaire 2003; Armas & Pugnaire 2005). Although there are fewer experimental tests of the effect of spatial structure (Stoll & Prati 2001; Monzeglio & Stoll 2005), there is convincing evidence that intraspecific aggregation of plants in experimental communities can promote species coexistence (Stoll & Prati 2001; Monzeglio & Stoll 2005; Mokany *et al*. 2008). The patterns of plants in communities have also been linked to the distribution of soil resources (MacMahon

1997), the effect of disturbances such as grazing (Rebollo *et al*. 2002), and plant

population dynamics (Fowler 1986; Franco & Nobel 1988; Valiente-Banuet *et al*. 2006).

Ecological processes in turn affect the spatial pattern of the affected individuals.

Regular patterns have been historically viewed as the result of intense competition for

limited resources, such as available water or soil resources (King & Woodell 1973;

Phillips & MacMahon 1981; Skarpe 1991). Random patterns may be a direct result of

ecological processes such as habitat heterogeneity (Tirado & Pugnaire 2003), or may

emerge temporarily when aggregated patterns shift to regular patterns because of density-

dependent mortality (Prentice & Werger 1985). Aggregated patterns are actually quite

common, especially in more diverse plant communities (Perry *et al*. 2009). Intraspecific

aggregation has been attributed to environmental heterogeneity (Schenk *et al*. 2003; Perry

et al. 2009), seed dispersal (Schurr *et al*. 2004), and plant interactions, (Phillips &

MacMahon 1981; Eccles 1999; Tirado & Pugnaire 2003). In more arid communities,

interspecific aggregation of forbs, grasses, and juvenile woody plants around larger

shrubs and trees is often interpreted as evidence of facilitation (e.g. review by Brooker *et

al*. 2008). In physically stressful environments, plants that facilitate one another often do

so by ameliorating harsh abiotic conditions (e.g. reducing evapotranspiration) (Haase

1996; Armas & Pugnaire 2005). Communities that are structured by positive plant

interactions often have plant spatial patterns that are characterized by multispecific plant

aggregations (Eccles *et al*. 1999; Kéfi *et al*. 2007; Valiente-Banuet & Verdú 2008).

As a result of the link between spatial patterns and ecological processes, studies of

plant patterns have often been conducted under the assumption that the results of pattern

analysis can give information on the predominant ecological processes in these

communities. In this context it is important to state that in principle it is not possible to derive a process from a pattern, since the same spatial structure can be a result of different processes (Schurr 2004; McIntire & Fajardo 2009). However, ecologically informed *a priori* hypotheses on the spatial pattern itself can be statistically tested and can help to approach an understanding of the underlying processes. For example, Fajardo & McIntire (2007) analyzed spatial patterns of forest growth to evaluate multiple competing hypotheses regarding the importance of competition and microsite variability in *Pinus ponderosa* plantations.

Generally pattern studies involve the collection and analysis of spatial data on one or more species within a community, and the common approach has been to test for regular, random, or aggregated plant spatial patterns of the species of interest. A wide variety of methods have been devised to map individual plants within communities, including quadrat sampling (Phillips & MacMahon 1981), progressive mapping (Rohlf & Archie 1978; Boose *et al*. 1998), triangulation (Schurr *et al*. 2004), and remote sensing and interpretation of aerial photography (Strand *et al*. 2006). All mapping methodologies have some associated level of spatial measurement error that should be quantified and reported. This error, a function of the precision of the methodology, may have profound effects on subsequent data analysis and interpretation. In a study of the effect of data quality on the results of point pattern analysis via second order spatial statistics, Freeman & Ford (2002) concluded that measurement error produced by mapping techniques and equipment significantly affected the detection of both inhibition and aggregation within plant communities. Specifically, the authors noted that the effect of measurement errors were inversely proportional to the scale of interaction between mapped plants, such that

measurement errors could obscure fine-scale inhibition while also causing an overestimation of the scale of aggregation.

Certain methodologies, such as the use of a tape measure and hand compass or an off-the-shelf GPS unit, may have associated spatial errors of $\geq$ 1m that may render inappropriate any fine-scale (e.g. < 1m) analysis of plant spatial patterns. More precise methods have been used to map vegetation (Schenk *et al*. 2003), but may require multiple field personnel and/or surveyor-established control points in addition to being time-consuming and cumbersome in the field (Lavine 2003). The challenges associated with mapping plant communities using more precise methodologies means that large sample sizes may be difficult to obtain, or that larger areas may be difficult to exhaustively map. Large sample sizes may be crucial, since small sample sizes may have large standard deviations that prevent meaningful comparisons with null models during spatial analysis (Perry *et al*. 2008). An ideal mapping methodology would be both rapid and precise in order to minimize spatial error and enable efficient collection of larger sample sizes appropriate for significance testing and generalizing results back to the community at large.

In this study, our primary objective was to develop a relatively novel approach to obtaining large datasets of high-quality spatial data in Great Basin shrub-dominated plant communities in the Western United States. This GPS-based approach is both rapid and highly precise, requires only a single person to operate, and is feasible in any terrestrial plant community without significant tree cover where individual plants are discernable. Our secondary objective was to demonstrate one potential application of this methodology by using second-order spatial statistics to investigate the spatial structure of

the shrub community. Under the general hypothesis that the shrub community under study would be characterized by localized aggregation, a common feature of other semi-arid shrublands (Schenk *et al*. 2003; Tirado & Pugnaire 2003), we used a recently developed spatial statistic (Schiffers *et al*. 2008) to test if shrubs were significantly aggregated (a) independent of species; (b) within individual species (intraspecific aggregation); and (c) between species (interspecific aggregation).

Methods

Data Collection

The study site was located on a grazing allotment in a mixed Great Basin shrub community east of the Vernon Hills in the southern end of Rush Valley, Tooele Co., UT, USA (longitude -112.36125, latitude 40.10253). A total of five shrub taxa were present, representing the two plant families Asteraceae and Chenopodiaceae: Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young ; Asteraceae), broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britton & Rusby; Asteraceae), spineless horsebrush (*Tetradymia canescens* DC.; Asteraceae), winterfat (*Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit; Chenopodiaceae), and shadscale saltbush (*Atriplex confertifolia* (Torr. & Frém.) S. Watson; Chenopodiaceae). *G. sarothrae* is often considered a sub-shrub, but we followed other authors in including both shrubs and sub-shrubs in spatial analysis (Haase *et al*. 1996; Schenk *et al*. 2003). Other species present on-site included Indian ricegrass (*Achnatherum hymenoides* (Roem. & Schult.) Barkworth), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey),

halogeton (*Halogeton glomeratus* (M. Bieb.) C.A. Mey), cheatgrass (*Bromus tectorum*

L.), and various annual forbs.

A 39m by 39m plot was established in September 2008 and divided into 3-m

strips to facilitate data collection. The location and species of all shrubs in the plot were

collected using the ProMark3 GPS system, a survey-grade GPS unit that enables both

rapid and precise data collection. As used in this study, the ProMark3 is composed of a

base unit mounted on a fixed height tripod near the plot and a rover unit mounted on a

fixed height pole equipped with a bubble level. Once the base unit was activated, static

survey data were continuously collected for the base point at one second intervals. The

rover unit was placed at the main stem of each shrub, generally in the middle of the shrub

canopy, and data were collected for five seconds with a one second collection interval.

Base and rover data were processed against data from National Geodetic Survey

Continuously Operating Reference Stations (CORS) using GNSS Solutions software (v.

3.10.01, Magellan Navigation 2007).

<u>Data Analysis</u>

Spatial analysis was performed in R (R Development Core Team 2007) using

both base functions and the *spatstat* package for spatial analysis of point patterns (v.

1.14-7, Baddeley & Turner 2005). Density surfaces created for the plot-level and species-

specific point patterns strongly suggested that shrubs were inhomogeneously distributed

across the study region. In order to account for this heterogeneity while simultaneously

testing for aggregation, we implemented the recently developed K2 statistic (Schiffers *et

al*. 2008). While Ripley's K and the pair correlation statistic *g* are commonly used in

analyses of point pattern data, these statistics are based on the assumption that the point

pattern is homogenous in space (i.e., has a constant intensity across the study region;

Schiffers *et al*. 2008). Actual variation in intensity across the study area can result in

"virtual aggregation," in which bias in the estimated K- or g-statistics indicates stronger

positive autocorrelation than actually exists and obscures critical pattern information at

finer scales at which individual plants compete for water and soil resources (Wiegand &

Moloney 2004; Schiffers *et al*. 2008).

The K2 statistic is essentially the first derivative of the *g* statistic, and K2(r)

estimates are obtained by calculating the slope of the estimated *g* statistic over a range of

scales from $r + \Delta r$ to $r - \Delta r$:

$$\hat{K}2(r) = \frac{\hat{g}(r + \Delta r) - \hat{g}(r - \Delta r)}{2\Delta r}$$

Similar to the O-ring statistic (Wiegand & Moloney 2004), and in contrast to Ripley's K,

the K2 is noncumulative; i.e., the spatial pattern at finer scales does not influence the K2

statistic at broader scales as is the case with cumulative spatial statistics like Ripley's K

(Blanco *et al*. 2008).

The statistical significance of $\hat{K}2(r)$ values can be evaluated relative to pointwise

Monte Carlo simulation envelopes, constructed with the *envelope* function in the *spatstat*

package. Pointwise envelopes indicate the critical points for a Monte Carlo test that is

performed using a fixed value of *r*, where the null hypothesis (e.g. Complete Spatial

Randomness, or CSR) is rejected if the estimate of $\hat{K}2(r)$ lies outside the envelope at the

given value of *r* (Baddeley & Turner 2005). Significantly positive values of $\hat{K}2(r)$

indicate the upper limit of the scale range at which the pattern is regular; significantly

negative values indicate the upper limit of the scale range at which the pattern is

aggregated (Schiffers *et al*. 2008). Simulation envelopes differ from confidence

envelopes, and have been criticized for potentially leading to type I errors when values of

the evaluated function (e.g. K2) are close to values of the simulation envelopes

(Loosemore & Ford 2006; Blanco *et al*. 2008). This is less of a concern when using

noncumulative statistics (Loosemore & Ford 2006; Blanco *et al*. 2008); however, the

significance of small departures from the null model should be interpreted with caution

(Blanco *et al*. 2008). For this analysis, we constructed approximate 95% simulation

envelopes using the 10th highest and lowest values of K2(r) from 199 simulations of

CSR. While more sophisticated null models are available, we chose the straightforward

null model of CSR for the sake of simplicity.

Similarly, we used the K2 statistic to test for aggregation within each of the five

shrub species individually. In order to test for interspecific aggregation, we used the

software package Programita (Wiegand & Moloney 2004) that allowed for the fitting of

bivariate O-ring statistics coupled with appropriate null models to look for evidence of

spatial structure between all pairs (*i,j* and *j,i*) of shrub species present in the plot. That is,

all species pairs were analyzed as two distinct pairs, the distribution of species *i* relative

to species *j* and the distribution of species *j* relative to species *i*, for a total of 20 pairs.

The O-ring statistic evaluates the expected number of points of a pattern at increasing

distances (*r*) from an arbitrary point of a pattern. When used with an appropriate null

model and permutation procedures, positive and negative deviations of $\hat{O}_{ij}(r)$ indicate

second-order aggregation and regularity, respectively, between points of type *i* and *j* in a

point pattern dataset. Like the K2 statistic, the O-statistic is noncumulative and therefore

less prone to type I errors related to the construction of simulation envelopes. Two

contrasting types of null models are commonly fitted to bivariate point analyses:

independence and random labeling (Wiegand & Moloney 2004). Testing for

independence in a bivariate setting is more complicated than fitting a CSR null model to

a univariate process. The second-order structure associated with each pattern must be

preserved in the course of null model simulation, but the dependence between the two

patterns must be removed. Applying a random shift to pattern j while holding fixed

pattern i overcomes this hurdle and allows for a test for spatial structure between points

of type i and j. In this study, bivariate O-statistics were calculated for all pairs of shrub

species, with random shifts set as the null model. In each case, the locations of shrub

species i were held constant, while the locations of shrub species j were randomized (N_{sim}

= 199; 10th highest and lowest values of $\hat{O}_{ij}(r)$ used to construct simulation envelopes) in

order to test for significant spatial structure between the two species.

Results

      The GPS-based methodology was used to map the location and identity of 2358

individual shrubs within the study plot (Fig. 1). Data collection required approximately

16 field hrs, with data-post processing requiring an additional 1-2 hrs. After post-

processing, the spatial error (calculated in GNSS solutions using the least squares

method) associated with x,y coordinates of shrubs was calculated to be ≤ 0.02 m. *A.*

tridentata was the most common shrub in the plot, followed by *T. canescens*, *G.*

sarothrae, *A. confertifolia*, and *K. lanata* (Table 1). Mean shrub density was 1.56

shrubs/m^2, while densities of individual shrub species ranged from 0.19 shrubs/m^2 to 0.61

shrubs/m^2 (Table 1).

Spatial analysis revealed strong evidence of aggregation, independent of species

(Fig. 2a). This pattern was observed even after controlling for the effect of *A. tridentata*,

the most abundant shrub (data not shown). Aggregation was present at scales < 0.50m,

and there was no evidence of either aggregation or regularity at larger scales. There was

also strong evidence of intraspecific aggregation in two shrub species, *A. tridentata* and

K. lanata, at scales of < 0.50m (Fig. 2b, e). There was also suggestive evidence of

aggregation in *A. confertifolia* at a similar scale, while there was suggestive evidence of

both regularity and aggregation in *G. sarothrae* (at 0.10m < r < 0.25m and r = 0.50m,

respectively; Fig. 2c,e). By suggestive, we mean that the values of the K2 function were

close to the values of the null model, and that results should be interpreted with caution

(Blanco et al. 2008). There was no evidence of either aggregation or regularity in *T.*

canescens (Fig. 2f).

There was evidence of interspecific aggregation for only two of the 20 pairs of

species. *A. tridentata* was aggregated relative to *A. confertifolia*, and *A. confertifolia* was

aggregated relative to *G. sarothrae* (Fig. 3). For both species pairs, aggregation was

detected at a scale of approximately 0.2 m. There was suggestive evidence of regularity

between *A. tridentata* and *A. confertifolia* and aggregation between *A. confertifolia* and

G. sarothrae at larger scales.

Discussion

<u>Data collection and analysis</u>

Analysis of plant spatial patterns is a popular technique in plant ecology, but there

are challenges associated with rapidly obtaining large samples of precise plant locations.

Historically, the classic tradeoff related to spatial data collection has been between speed

and precision. In this study, however, the use of the ProMark3 survey-grade GPS system

allowed for the rapid and precise collection of species and location data for more than

2300 shrubs of five species in a semi-arid, mixed shrub community in the Great Basin

portion of the western U.S. Although past authors have provided convincing evidence of

statistically significant plant spatial patterns, larger and more precise datasets could lead

to better generalizations about the larger plant communities and processes at work

therein. An additional advantage of the ProMark3 is that the base unit may be located

several kilometers (up to ~15 km under ideal conditions) away from the site of data

collection, and multiple rover units can be used at the same time with a single base unit.

Furthermore, the mobility of the rover unit means that data may be collected along

uneven topography that might otherwise render spatial data collection difficult or

unfeasible altogether. Drawbacks include the usual difficulties with using GPS under tree

canopies, the initial expense of purchasing the system, and the need to post-process the

data (albeit a relatively simple process usually requiring less than an hour). Given the

difficulties of collecting large spatial datasets in mixed-species communities, however,

the speed and precision associated with the ProMark3 GPS system outweigh the few

disadvantages. Barring significant tree cover, the methodology presented here can be

easily adapted for a wide variety of plant communities where individual plants are distinguishable.

Since the primary goal of this study was to demonstrate the speed and precision by which point pattern data may be collected via a GPS-based methodology, we chose not to collect size class data on shrubs within the study plot. Our approach is similar to other recent studies of plant spatial patterns in which the assumption is made that plant locations are adequately represented as zero-dimensional points (Perry *et al.* 2009). Size class data is often an important component of spatial datasets, and is used to test more sophisticated hypotheses related to plant interactions (Wiegand *et al.* 2006). Such data could be collected by a second observer working in tandem with the GPS person or at a later date by using the resultant community map as a guide to relocate and measure individual plants.

The collection and analysis of precise spatial data represents only one of the potential applications for the GPS-based community mapping methodology. For example, long-term plots could be established in shrubland communities across the western U.S. in order to evaluate the effects of climate change on plant spatial patterns, species coexistence, and population dynamics across ecological gradients and/or in communities with different species compositions. Precise spatial data would allow for the monitoring of recruitment and mortality necessary for population modeling, and changes in plant spatial patterns could be linked to ecological processes such as disturbance, plant interactions, and fluctuations in environmental heterogeneity. From a management perspective, our methodology could be used to accurately map the locations of rare or threatened plants across large expanses of terrain, in order to facilitate relocation and

measurement of individual plants as part of monitoring and conservation programs. An

additional advantage of our approach is that the spatial data integrate seamlessly with

GIS software, meaning that additional data (such as elevation, road networks, and land

cover) could be included in vegetation analyses.

Patterns and process

The aggregated shrub spatial patterns observed in this study of a semi-arid shrub

community may be the result of multiple ecological processes. Although carefully

designed observational and experimental studies are required to clearly elucidate the

processes creating plant spatial patterns, previous studies suggest that disturbance,

dispersal, environmental heterogeneity and/or facilitation may have led to the aggregated

spatial structure in the shrub community under study.

For example, the potential role of grazing in creating and maintaining shrub

spatial patterns in semi-arid shrublands cannot be overlooked (Kéfi *et al.* 2007). In this

study, five shrub taxa were present within the plot, which itself is part of an active

grazing allotment. While *A. tridentata*, *G. sarothrae*, and *T. canescens* are generally

regarded as poor forage for livestock, *A. confertifolia* and *K. lanata* are widely grazed in

Great Basin shrublands (Elmore 1976). There is a substantial body of literature that has

examined the effect of grazing on spatial heterogeneity (e.g. Adler *et al*. 2001;

HilleRisLambers *et al*. 2001; Seifan & Kadmon 2006; Blanco *et al*. 2008). A recent study

tested the role of grazing in spatial pattern formation in a Mediterranean scrub ecosystem

by correlating 40 years of shrub pattern data with grazing intensity (Seifan & Kadmon

2006). The degree to which grazing influenced shrub aggregation was thought to be a

result of the relative palatability of shrubs as compared to other plants in the community, and the degree of interference or facilitation between adult shrubs and other plants. In addition, indirect effects of grazing (such as trampling of seedlings and soil compaction) may also have significant and different effects on shrub spatial patterns.

Another alternative hypothesis to explain the widespread aggregation in this study is localized seed dispersal around parents resulting in seed limitation away from existing adults. Although seed shadows from primary dispersal are not known for these species, secondary movement across the surface is extensive (Chambers 2000), suggesting that short-distance dispersal is unlikely to explain the pattern. Even with extensive secondary movement, however, seeds might be disproportionately captured at the edge of the litter accumulating beneath shrubs, resulting in aggregations of recruits around existing adults.

In addition, environmental heterogeneity (e.g. patchy distribution of soil resources) may lead to the formation of aggregated shrub spatial patterns (Schenk *et al.* 2003; Tirado & Pugnaire 2003; Perry *et al.* 2008; Perry *et al.* 2009). Patchy resource distribution may occur as the result of the latent distribution of soil resources, or as a result of plant-soil interactions such as those that lead to the formation of "islands of fertility" (Schlesinger *et al.* 1990).

Lastly, aggregated shrub patterns in water-limited plant communities are often attributed to facilitation within and between shrub species. While the analysis of plant spatial patterns cannot fully explain the complexities of plant interactions, patterns that significantly deviate from random have often been used to infer the type and magnitude of plant interactions for one or more species within different plant communities. As researchers have continued to use spatial analysis to seek answers about the role of plant

interactions in water-limited regions, it has become increasingly apparent that facilitation

plays a critical role in structuring certain arid and semi-arid plant communities.

Aggregation of shrubs can have dramatic effects on survivorship, reproductive success,

plant performance, population dynamics, and coexistence of shrub species at multiple life

stages (Haase *et al*. 1996; MacMahon 1997; Tirado & Pugnaire 2003). However,

facilitation is most often detected among heterospecific species pairs and heterospecific

plant aggregations are often taken as evidence of facilitation (Eccles *et al*. 1999; Kéfi *et

al*. 2007; Valiente-Banuet & Verdú 2008). The degree of intraspecific aggregation that

was detected by K2 statistic suggests that shrub clusters in the community under study

are composed largely of conspecific individuals, with the exception of *A. tridentata* being

aggregated relative to *A. confertifolia* and *A. confertifolia* being aggregated relative to *G.

sarothrae*. Our results suggest that facilitation is not a dominant pattern-forming process

in the study community.

Interference may also influence shrub patterns within the community, although

little evidence of regular plant spatial patterns was detected. Regular patterns are often

interpreted as evidence of fine-scale interference between plants, a process that for more

than a century has been viewed as an important factor governing plant distribution

patterns in water-limited plant communities (Fowler 1986; Armas & Pugnaire 2005;

Miriti 2006). Only *G. sarothrae* showed any evidence of intraspecific regularity, and then

only at a relatively fine spatial scale. *G. sarothrae* individuals were aggregated at a

slightly broader spatial scale, implying that plants of this species form small, regularly

spaced clusters. Interspecific regularity was detected between *A. tridentata* and *A.

confertifolia*, but at scales greater than the scale at which aggregation was detected ($r =$

0.80 m and $r = 1.2$ m, see Fig. 2a). This result suggests that pairs or clusters of these

species are somewhat regularly spaced, implying a shift in pattern forming processes over

short distances. For example, it could be that net effect of plant-plant interactions

switches as a function of distance; over short spatial scales there may be net facilitation,

but with increasing distances from another shrub facilitation weakens while competition

for water and soil resources may remain a strong force due to the extensive root systems,

resulting in a switch to net interference.

Each of the above mentioned processes (disturbance, dispersal, environmental

heterogeneity, and plant interactions) may have acted individually or in concert with

other processes to produce the spatial patterns detected in this study. The incorporation of

shrub size class data would allow for more sophisticated spatial analysis that could better

elucidate the role of individual processes, and field experiments addressing the effect of

each process on shrub spatial structure may also be required.

Conclusion

In this study, the use of the ProMark3 survey-grade GPS system allowed for the

rapid and precise collection of shrub spatial data in a semi-arid, mixed-shrub community

within the Great Basin in the western United States. The resulting point pattern was

analyzed in R and Programita using spatial statistics that included the recently developed

K2 statistic, coupled with null models and permutation procedures that allowed for

significance testing. Analysis revealed that aggregation was the predominant spatial

pattern associated with shrubs, independent of species. Furthermore, intraspecific

aggregation was observed in four of the five study species. Interspecific aggregation was

also observed, although only two of 20 shrub pairs were aggregated. These results

demonstrate the utility of combining new data collection techniques with both traditional

and novel spatial analyses, and also suggest future studies to determine the ecological

processes by which shrub aggregation is produced in the study community.

References

Adler, P. B., Raff, D. A. & Laurenroth, W. K. 2001. The effect of grazing on the spatial
heterogeneity of vegetation. Oecologia 128:465-479.

Armas, C. & Pugnaire, F. I. 2005. Plant interactions govern population dynamics in a
semi-arid plant community. J. Ecol. 93:978-989.

Baddeley, A. J. & Turner, R. 2005. Spatstat: an R package for analyzing spatial point
patterns. J. Stat. Softw. 12:1-42.

Blanco, P. D., Rostagno, C. M., del Valle, H. F., Beeskow, A. M. & Wiegand, T. 2008.
Grazing impacts in vegetated dune fields: predictions from spatial pattern
analysis. Rangeland Ecol. Manag. 61:194-203.

Boose, E. R., Boose, E. F. & Lezberg, A. L. 1998. A practical method for mapping trees
using distance measurements. Ecol. 79:819-827.

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler,
G., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll,
L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F.,
Quiroz, C. L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. & Michalet, R.
2008. Facilitation in plant communities: the past, the present, and the future. J.
Ecol. 96:18-34.

Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecol. Appl. 10:1400-1413.

Eccles, N. S., Esler, K. J. & Cowling, R. M. 1999. Spatial pattern analysis in Namaqualand desert plant communities: evidence for general positive interactions. Plant Ecol. 142:71-85.

Elmore, F. H. 1976. Shrubs and trees of the Southwest Uplands. Southwest Parks and Monuments Association.

Fajardo, A. & McIntire, E. J. B. 2007. Distinguishing microsite and competition processes in tree growth dynamics: an a priori spatial modeling approach. Amer. Nat. 165:647-661.

Fowler, N. 1986. The role of competition in plant communities in arid and semi-arid regions. Ann. Rev. Ecol. Syst. 17:89-110.

Franco, A. C. & Nobel, P. S. 1988. Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. Ecol. 69:1731-1746.

Freeman, E. A. & Ford, E. D. 2002. Effects of data quality on analysis of ecological pattern using the K(d) statistical function. Ecol. 83(1):35-46.

Haase, P., Pugnaire, F. I., Clark, S. C. & Incoll, L. D. 1996. Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. J. Veg. Sci. 7:527-534.

HilleRisLambers, R., Rietkerk, M., Van den Bosch, F., Prins, H. T. H. & De Kroon, H. 2001. Vegetation pattern formation in semi-arid grazing systems. Ecol. 82:50-61.

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A. & de Ruiter, P. C. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213-217.

King, T. J. & Woodell, S. R. J. 1973. The causes of regular pattern in desert perennials. J. of Ecol. 61:761-765.

Lavine, A., Gardner, J. N. & Reneau, S. L. 2003. Total station geologic mapping: an innovative approach to analyzing surface-faulting hazards. Eng. Geol. 70:71-91.

Loosmore, N. B. & Ford, E. D. 2006. Statistical inference using the G or K point pattern spatial statistics. Ecol. 87:195-1931.

MacMahon, J. A. 1997. Ecological restoration. In: Meffe GK *et al*. (eds), Principles of conservation biology, Sinauer Associates, Inc., Sunderland, pp 479-511.

Magellan Navigation, Inc. 2007. GNSS solutions 3.10.01. http://pro.magellangps.com

McIntire, E. J. B. & Fajardo, A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. Ecol. 90:46-56.

Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. J. Ecol. 94:973-979.

Mokany, K., Ash, J. & Roxburgh, S. 2008. Effects of spatial aggregation on competition, complementarity, and resource use. Austral Ecol. 33:261-270.

Monzeglio, U. & Stoll, P. 2005. Spatial patterns and species performance in experimental plant communities. Oecologia 145:619-62.

Perry, G. L. W., Enright, N. J., Miller, B. P. & Lamont, B. B. 2008. Spatial patterns in species-rich sclerophyll shrublands of southwestern Australia. J. Veg. Sci. 19:705-716.

Perry, G. L. W., Enright, N. J., Miller, B. P. & Lamont, B. B. 2009. Nearest-neighbor interactions in species-rich shrublands: the roles of abundance, spatial patterns and resources. Oikos 118:161-174.

Phillips, D. L. & MacMahon, J. A. 1981. Competition and spacing patterns in desert
    shrubs. J. Ecol. 69:97-115.

Prentice, I. C. & Werger, M. J. A. 1985. Clump spacing in a desert dwarf shrub
    community. Vegetatio 63:133-139

R Development Core Team 2007. R: a language and environment for statistical
    computing. R foundation for statistical computing, Vienna, Austria,
    http://www.R-project.org.

Rebollo, S., Milchunas, D. G., Noy-Meir, I. & Chapman, P. L. 2002. The role of a spiny
    plant refuge in structuring grazed shortgrass steppe plant communities. Oikos
    98:53-64.

Rohlf, F. J. & Archie, J. W. 1978. Least-squares mapping using interpoint distances.
    Ecol. 59:126-132.

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M.,
    Virginia, R. A. & Whitford, W. G. 1990. Biological feedbacks in global
    desertification. Science 247:1043-1048.

Schenk, H. J., Holzapfel, C., Hamilton, J. G. & Mahall, B. E. 2003. Spatial ecology of a
    small desert shrub on adjacent geological substrates. J. Ecol. 91:383-395.

Schiffers, K., Schurr, F. M., Tielbörger, K., Urbach, C., Moloney, K. & Jeltsch, F. 2008.
    Dealing with virtual aggregation – a new index for analyzing heterogeneous point
    patterns. Ecography 31:545-555.

Schurr, F. M., Bossdorf, O., Milton, S. J. & Schumacher, J. 2004. Spatial pattern
    formation in semi-arid shrubland: a priori predicted versus observed pattern
    characteristics. Plant Ecol. 173:271-282.

Seifan, M. & Kadmon, R. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a Mediterranean scrub community. Basic and Applied Ecol. 7:496-506.

Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. J. Veg. Sci. 2:565-572.

Stoll, P. & Prati, D. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. Ecol. 82:319-327.

Strand, E. K., Vierling, L. A., Smith, A. M., Bunting, S. C., Hann, D. B. & Gessler, P. E. 2006. Wavelet estimation of plant spatial patterns in multitemporal aerial photography. Int. J. Remote Sens. 27:2049-2054.

Tielbörger, K., Kadmon, R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecol. 81:1544-1553.

Tirado, R. & Pugnaire, F. I. 2003. Shrub spatial aggregation and consequences for reproductive success. Oecologia 136:296-301.

Valiente-Banuet, A., Verdú, M., & Callaway, R. M. 2006. Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. Proc. Natl. Acad. Sci. 103:16812-16817.

Valiente-Banuet, A. & Verdú, M. 2008. Temporal shifts from facilitation to competition occur between closely related taxa. J. Ecol. 96:489-494.

Wiegand, T. & Moloney, K. A. 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104:209-229.

Wiegand, T., Kissling, W. D., Cipriotti, P. A., & Aguiar, M. R. 2006. Extending point pattern analysis to objects of finite size and irregular shape. J. Ecol. 94:825-837.

Table 1. Summary statistics for shrub spatial data by taxon. $N_{species}$ = sample size per species; Proportion = % of total; $\lambda_{species}$ = density (shrubs / m^2). N_{total} = 2358.

Species	$N_{species}$	Proportion	$\lambda_{species}$
A. tridentata	918	0.39	0.61
A. confertifolia	307	0.13	0.20
T. canescens	602	0.26	0.40
K. lanata	179	0.08	0.19
G. sarothrae	352	0.15	0.23

All species   Artemisia   Atriplex

Gutierrezia   Tetradymia   Krascheninnikovia
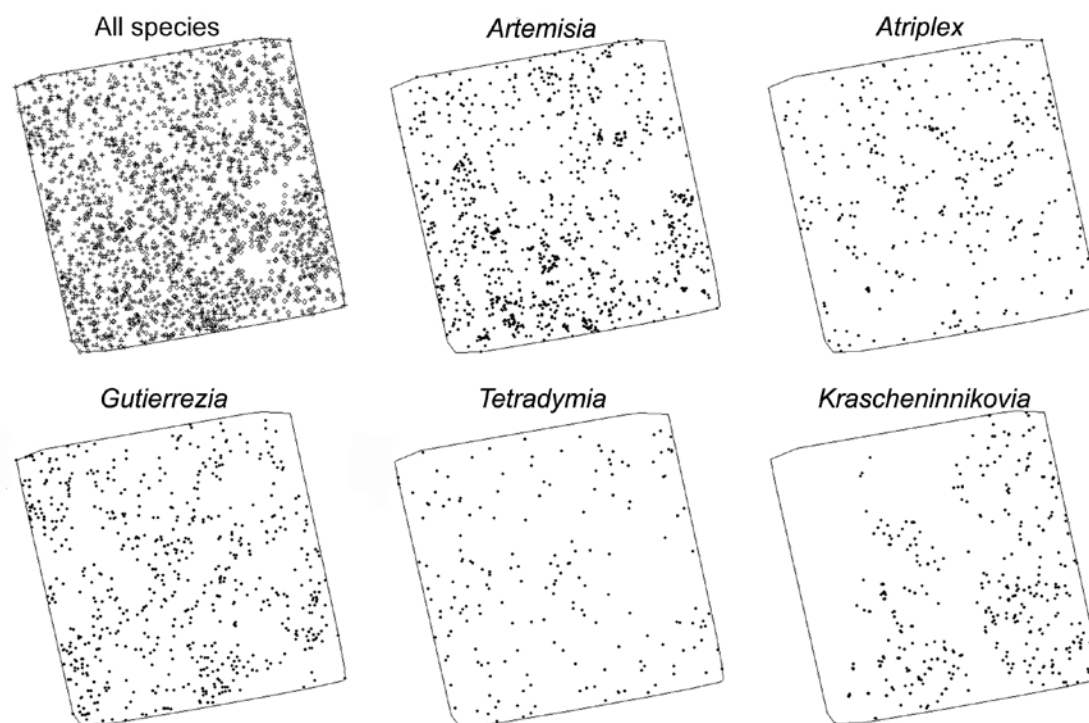
Fig. 1 Map of study plot (39m x 39m), showing locations of all shrub individuals (upper left) and maps detailing the locations of individuals from each of the five shrub species.
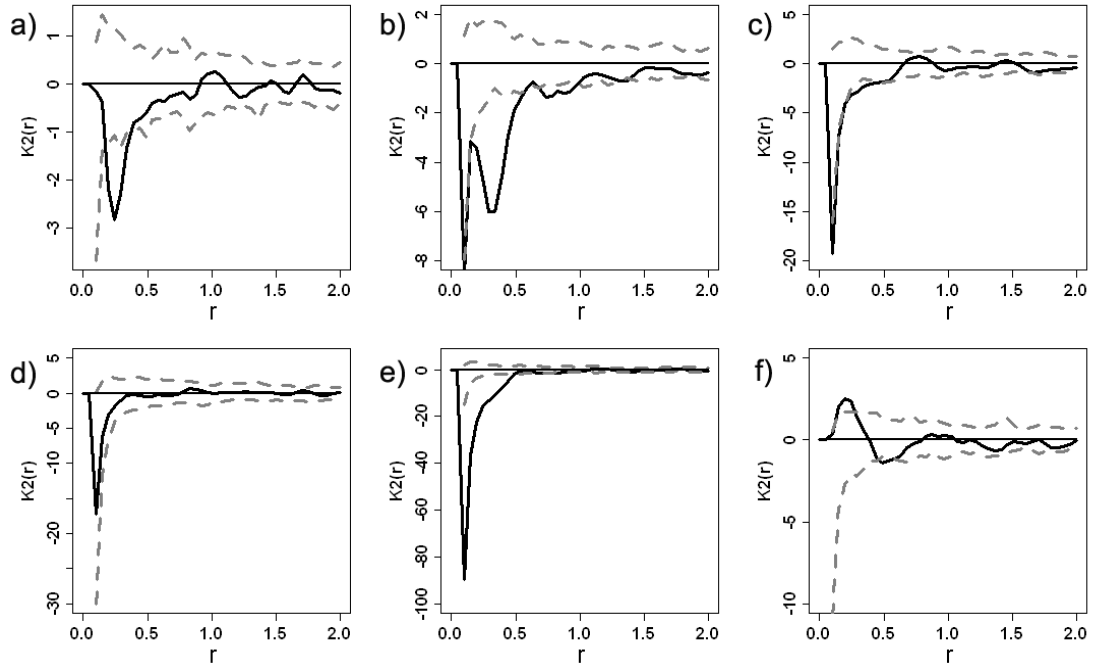
Fig. 2 K2 plots for a) all species combined; b) *Artemisia tridentata*; c) *Atriplex*

confertifolia; d) *Krascheninnikovia lanata*; e) *Gutierrezia sarothrae;* and f) *Tetradymia*

canescens. Dotted lines indicate 95% Monte Carlo simulation envelopes (n_{sim} = 199).

Significant aggregation is indicated by negative peaks in the solid black line that extend

beyond the boundaries of the simulation envelopes, while regularity is indicated by

positive peaks extending beyond the boundaries.
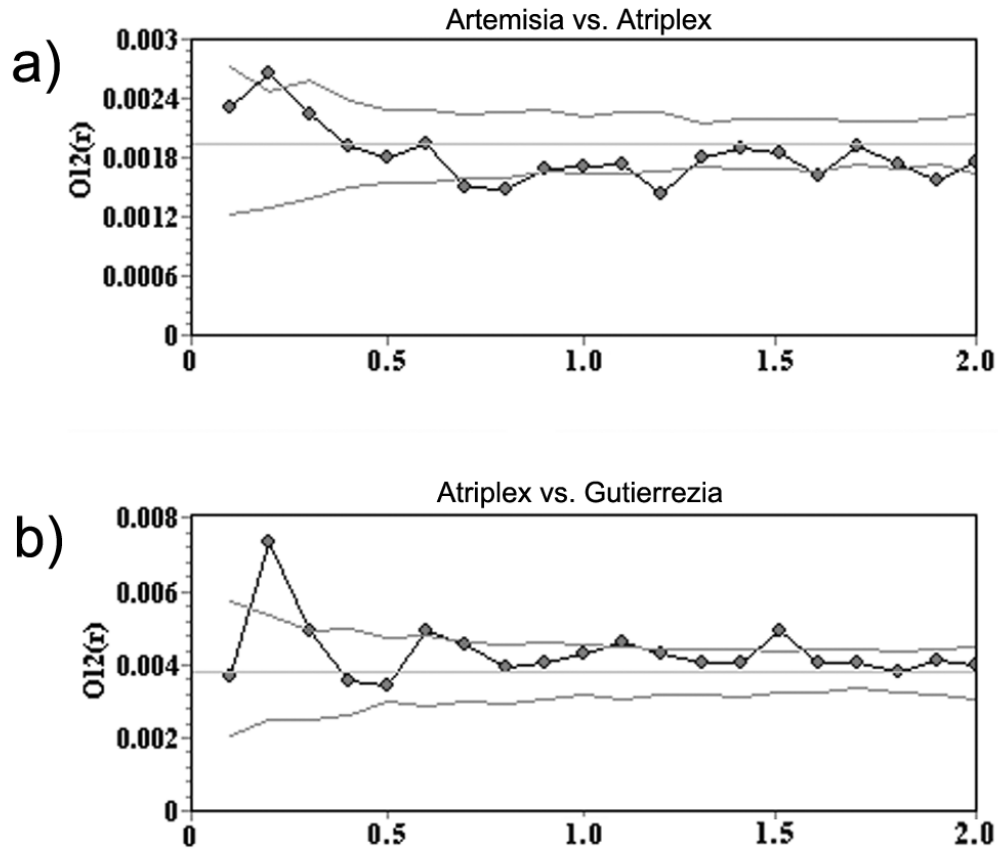
Fig. 3 Plots of bivariate O-ring statistics for two species pairs with significant spatial structure; a) *A. tridentata* relative to *A. confertifolia*; b) *A. confertifolia* relative to *G. sarothrae*. Values of x-axis are in 0.1m increments. Gray lines are 95% Monte Carlo simulation envelopes ($n_{sim} = 199$). Both plots show significant aggregation of shrub species pairs at a distance of approximately 0.20m (above the upper simulation envelope). In plot a), there is also suggestive evidence of regularity at larger scales, while in plot b) there is suggestive evidence of aggregation at larger scales.

CHAPTER III

INDIVIDUAL SPECIES-AREA RELATIONSHIPS AND SPATIAL

PATTERNS OF SPECIES DIVERSITY IN A GREAT

BASIN, SEMI-ARID SHRUBLAND

Abstract

Traditional biodiversity metrics operate at the level of a plant community but do not capture spatial variation in diversity from a 'plant's-eye view' of a community. Recently-developed statistics consider the spatial patterns of plants as well as the number and distribution of species in local plant neighborhoods to quantitatively assess multispecies spatial patterns from a "plant's-eye view." We used one such statistic, the individual species-area relationship (ISAR), to assess spatial patterns of species diversity in a Great Basin (USA) semi-arid shrubland through an analysis of a spatial dataset on shrub species and locations. In conjunction with appropriate null models, the ISAR blends species-area relationships with second-order spatial statistics to measure the expected species richness in local neighborhoods of variable size around the individuals of a focal species within a community. We found that, contrary to a previous analysis using more traditional methods, the community was well-mixed with a typical shrub surrounded on average by 4.9 shrub neighbors of 2.1 species at a neighborhood scale of 1.0 m. We also found statistically significant fine-scale variation in diversity patterns, such that neighborhoods of two species were more diverse than expected by a heterogeneous Poisson null model that accounted for larger-scale habitat heterogeneity. However, this effect was caused by intraspecific aggregation of these species and was not

due to positive interspecific association. Contrary to previous findings in other semi-arid shrublands, our analysis suggests that the spatial pattern of the shrub community was not significantly structured by interspecific facilitation. This result supports growing evidence for balanced species patterns of adult plants in multispecies communities. Our approach may be used in other communities to describe complex multispecies spatial patterns, quantify species-specific associations with diversity patterns, and to generate hypotheses regarding relationships between patterns and community-structuring processes.

Introduction

Classic measures of biodiversity consider species richness and evenness at the level of a plant community, while giving little weight to diversity at the scale of individual plant neighborhoods (Shimatani and Kubota 2004, Wiegand et al. 2007a). For example, the traditional species-area relationship (SAR) describes how the number of species in a community changes with sampling area (He and Legendere 2002) and can be considered a location-related summary characteristic because it is determined with reference to sampling points that are chosen independently of plant locations (Illian et al. 2008). However, many processes that structure plant communities (e.g. plant interactions) occur over fine scales such as local plant neighborhoods (Illian et al. 2009), which suggests conducting analyses from the "plant's-eye view" (Turkington and Harper 1979, Law et al. 2009). Community-level analyses may therefore obscure interesting patterns in diversity that may be fundamental to understanding plant-plant interactions (Wiegand et al. 2007a), dispersal mechanisms (Wiegand et al. 2009), species coexistence (Illian and

Burslem 2007, Law et al. 2009), or in developing vegetation management strategies
(Shimatani 2001). Recently, novel statistics have been developed that allow for more
advanced analyses of the spatial patterns of diversity. These statistics consider the pattern
of individual plants as well as the number and distribution of species, combining diversity
metrics and point pattern analyses in order to quantitatively assess aspects of multispecies
spatial patterns from the "plant's-eye view" (Shimatani 2001, Shimatani and Kubota
2004, Wiegand et al. 2007a). These techniques also address the long-standing challenge
in spatial ecology of describing multispecific plant patterns without resorting to
numerous bivariate statistics (Wiegand et al. 2007a,b, Illian et al. 2009), and are being
used to elucidate new connections between diversity patterns and ecological processes in
plant communities such as mixed hardwood forests (Shimatani 2001), subtropical rain
forests (Shimantani and Kubota 2004), tropical rain forests (Wiegand et al. 2007a) and
high-diversity semi-arid shrublands (Illian et al. 2009). Such work is an important
contribution to the efforts of ecologists to understand the processes that structure
communities and promote species coexistence in the face of global declines in
biodiversity (Illian and Burslem 2007, Illian et al. 2009).

One of the most promising new spatial statistics is the individual species-area
relationship (ISAR; Wiegand et al. 2007a). ISAR is the expected number of species
within circular areas of radius *r* around a randomly chosen individual of the target species
t. The function was termed the individual species-area relationship because, in contrast to
the SAR, the sampling areas of the ISAR are centered on the locations of a focal species.
The SAR is thus linked to the species richness within neighborhoods around a focal
species (called in the following "neighborhood diversity") and therefore is a "point-

related" summary characteristic (Illian et al. 2008) that summarizes important

characteristics of diversity from the "plant's-eye view." For a species pool (1,…,S), the

ISAR can be estimated as:

$$ISAR(r) = \sum_{j=1}^{S}[1 - P_{tj}(0,r)]. \quad (1)$$

$P_{tj}(0, r)$ is the emptiness probability that species j was not present in the circles with

radius r around individuals of the target species t. If $a = \pi r^2$, then the ISAR function can

be expressed in terms of circular area a to resemble the common species-area relationship

(Wiegand et al. 2007a). The ISAR function has been used to assess species associations

in tropical forests (Wiegand et al. 2007a), but can be adapted to other plant communities

in which plants occur as discrete individuals whose pattern can be mapped.

The ISAR function can be used to detect spatial patterns in diversity from the

perspective of individual plants and to relate them to underlying mechanisms. Species

that accumulate an over-representative proportion of species richness in their local

neighborhoods have been termed diversity "accumulators," while species with less

diverse neighborhoods than expected have been termed diversity "repellers" (Wiegand et

al. 2007a). The shape of the ISAR function can be influenced by three basic mechanisms:

plant-plant interactions, plant-environment interactions, and the spatial pattern of the

focal species. Analyzing plant patterns using the ISAR function and appropriate null

models can disentangle the effects of each factor to some extent, giving insight into

ecological processes acting to structure the community under study. For example, if net

interactions between a focal species and other species are positive relative to the focal

species' effect on itself, then the focal species would likely have more diverse

neighborhoods than expected by chance; conversely, net negative interactions between a focal species and other species would likely result in less diverse neighborhoods than expected by chance. In the case of weak or balanced positive and negative interactions, local neighborhoods would not be expected to depart from neutral ISAR curves (Wiegand et al. 2007a). However, the ISAR does not isolate specific pairwise interactions; therefore a species may appear on balance to be "neutral" even when some of its pairwise interactions are strong. Such effects can only be captured with complementary pairwise analyses (e.g.Wiegand et al. 2007a,b).

Similar effects on the ISAR function can be observed if the neighborhood diversity in the preferred habitat of the focal species is above or below average due to plant-environment interactions. As is common practice with spatial pattern analyses, the use of appropriate heterogeneous null models can account of the effects of habitat association (Wiegand and Moloney 2004, Wiegand et al. 2007a). The pattern of the focal species may also influence the shape of the ISAR function if the focal species is locally dominant (reducing neighborhood diversity), or if there is a strong univariate effect [i.e., $P_{tt}(r)$ in equation 1]. This effect may be diagnosed and accounted for by calculating the ISAR function with and without counting the focal species, in order to determine if observed accumulator effects are artifacts of focal species pattern as opposed to signals of interspecific aggregation and potentially facilitation.

We used the ISAR framework to analyze spatial patterns of species diversity and to better understand pattern-forming processes in a semi-arid shrubland in the Great Basin region of the western U.S. Globally, the processes that structure semi-arid shrublands in space and time are key areas of research, especially processes that influence

species coexistence in more diverse shrublands (e.g. Tirado and Pugnaire 2003, Illian et al. 2009, Perry et al. 2009, see chapter 2). Non-random spatial patterns are common features of semi-arid shrublands (e.g. Schenk et al. 2003, Tirado and Pugnaire 2003, Illian et al. 2009, see chapter 2), and are often attributed to ecological processes presumed to influence pattern formation, community dynamics, and species coexistence (Tirado and Pugnaire 2003, Seifan and Kadmon 2006, Perry et al. 2009, Illian et al. 2009). For example, interspecific aggregations of plants are often interpreted as a result of positive plant interactions that are generally considered to play a prominent role in semiarid plant community dynamics because of harsh climate and scarce resources in these environments (Schlesinger et al. 1990, Kéfi et al. 2007, Pugnaire et al. 2011). ISAR analysis provides a means to test if the spatial pattern of shrubs in the semi-arid shrub community under study conserves a signal of positive plant interactions. After accounting for the effects of habitat association and focal species density, less diverse shrub neighborhoods than expected by the null model would suggest that shrub neighborhoods were largely monospecific and were structured by processes leading to intraspecific aggregation. More diverse shrub neighborhoods than expected would suggest the community under study was structured more by processes leading to positive interspecific associations (e.g. facilitation). Each scenario has important implications for shrub species coexistence in the semi-arid shrubland under study.

Materials and Methods

Study system

The study site was located on a grazing allotment in a semi-arid Great Basin shrub community in the southern end of Rush Valley, Tooele Co., UT, USA (UTM coordinates 386086.9 E, 4442770.5 N). Five co-dominant shrub taxa were present: *Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle & Young), *Gutierrezia sarothrae* (Pursh) Britton & Rusby, *Tetradymia canescens* (DC.), *Krascheninnikovia lanata* (Pursh) A. Meeuse & Smith, and *Atriplex confertifolia* (Torr. & Frém.) S. Watson. A 39 m × 39 m plot was established on level ground in September 2008, and the highly accurate (± 2 cm spatial error) locations of all shrubs (N=2,359) were determined using a survey-grade GPS system (Fig. 4, see chapter 2 for details on site characteristics and data acquisition).

ISAR analysis

Inference for a given focal species *t* had to be made conditionally on the spatial pattern of all other species since the goal was to reveal if individuals of the focal species were associated with species richness in their neighborhoods. For this purpose, only individuals of the focal species were relocated using appropriate null models (see below), and neighborhood diversity in their new locations was measured and compared with the observed neighborhood diversity.

Because not all shrub patterns in the study community were homogeneous (Fig. 4, see chapter 2), heterogeneous null models were required to approximately separate first and second-order effects. With a homogeneous Poisson null model (complete spatial randomness or CSR, Wiegand and Moloney 2004) each location in a study plot would

have the same chance to receive a relocated individual. This null model is thus sensitive

to both potential first-order effects of habitat association of the focal species and potential

second-order effects such as plant interactions. However, the heterogeneous Poisson null

model can be used to account for larger-scale habitat association (Wiegand et al. 2007a,b)

such that individuals are relocated not over the entire plot but only within a smaller

neighborhood with radius R in which direct plant-plant interactions are expected to occur.

This null model therefore accounts for broader-scale variability in habitat suitability

(because the entire neighborhood will have approximately the same suitability), but

potential effects of small-scale plant-plant interactions are removed by randomly

relocating of plants within their R neighborhood. However, this test assumes separation

of scales (Wang et al. 2010) and cannot therefore separate fine-scale habitat association

from plant interactions. In our study, we selected a neighborhood size of $R = 4$ m that was

somewhat larger than the expected range of direct shrub-shrub interactions. For the

technical implementation of this null model, see Wiegand et al. (2007a,b).

Following the methodology of Wiegand et al. (2007a), we calculated the ISAR for

each of the five shrub species up to a maximum distance (r_{max}) of 4.0 m with a spatial

resolution of 5 cm. To test for the effects of focal species dominance, we repeated each

ISAR analysis with and without including the focal species. This distance range was

dictated by the choice of the neighborhood radius $R = 4$ m in the heterogeneous Poisson

null model; at larger distances the ISAR will not capture significant effects because larger

scale effects are held constant by this null model. The 4 m distance was sufficient to

encompass both immediate shrub neighborhoods and the surrounding area, allowing for

the examination of how diversity patterns changed with increasing distance from the

center of shrubs. In order to determine if local shrub neighborhoods were significantly more or less diverse than expected by chance, we constructed Monte Carlo simulation envelopes based on 199 simulations of the heterogeneous Poisson null model. If the empirical *ISAR(r)* was larger at a given scale *r* than the fifth highest *ISAR(r)* from 199 null model simulations, the species was regarded as having a more diverse local neighborhood at scale *r* than expected by the null model (approximate α = 0.05) (Wiegand et al. 2007a). If the empirical *ISAR(r)* was smaller at a given scale *r* than the fifth lowest *ISAR(r)* from the 199 null model simulations, the species was regarded as having a less diverse local neighborhood at scale *r* than expected by the null model. Minor deviations (i.e., weakly significant results) of the estimated *ISAR(r)* relative to the simulation envelopes were interpreted with caution due to the problem of simultaneous inference (Loosmore and Ford 2006). To avoid this problem when assessing the fit of the empirical ISAR curves for the null model over the 0-4 m distance interval, we used goodness-of-fit (GoF) tests based on Cramer von Mises statistics (Loosmore and Ford 2006, Perry et al. 2006, Wiegand et al. 2007a).

In order to facilitate interpretation of the results of the ISAR analysis, we analyzed the pattern of all shrubs with the pair correlation function *g(r)* (PCF; Stoyan and Stoyan 1994, Illian et al. 2008), which provides an intensity-normalized estimate of neighborhood density. The PCF can be defined by the quantity λ*g(r)* that is the expected number of points within distance *r* from the points of the pattern, where λ represents the point intensity (i.e., the number of points divided by area). Finally, we calculated the cumulative distribution function *D(r)* (also termed Diggle's *G*) of the distances *r* to the nearest neighbor of each shrub (Illian et al. 2008).

Results

Community-level spatial structure

The shrub density within the study plot was 1.56 individuals/m^2, meaning that each individual shrub had an average of 0.67 m^2 of space. The mean distance to the nearest neighbor was 0.37 m, and all shrubs had their nearest neighbor within 1 m (Fig. 5B). Analysis of the pattern of all shrubs independent of species with the PCF revealed that local neighborhood densities were elevated by factor of 1.8 at a neighborhood scale of 20 cm, resulting in a density of 2.7 individuals/m^2 (Fig. 5A). This local clustering disappeared at scales approximately > 1 m. The pattern of all shrubs showed some heterogeneity at broader scales which are visible as gaps (Fig. 4). This is indicated by PCF values greater than the expected value of 1 at larger distances.

The ISARs for the five species were relatively similar (Fig. 5D) with differences usually not above 0.3 species within the explored ≤ 4 m neighborhoods (Fig. 5C). At neighborhoods > 2.5 m the difference among ISAR curves declined because most individuals were neighbored by individuals of all species. Neighborhood diversity increased up to 1.25 m almost linearly before saturating at 4 m neighborhoods (Fig. 5D). On average, shrubs in the study area had in small neighborhoods more heterospecific than conspecific neighbors. At a neighborhood of 1 m, for example, a given individual shrub was surrounded by approximately 5.9 shrub neighbors (the value of $\lambda K(r)$ at 1 m) that represented approximately 2.5 species (Fig. 5D). Within a 2.9 m neighborhood, a given individual shrub was surrounded by approximately 45 shrubs neighbors that represented approximately 4.75 species, or 95% of the total diversity. These results suggested that the

community was comprised of small, heterospecific clusters and was well-mixed at fine

spatial scales.

Species-specific comparisons with null models

Because the differences between the observed ISAR function and that of the

simulations of the heterogeneous Poisson null model were in general small, we present in

the following not $ISAR(r)$ but the difference $ISAR(r) - ISAR_{exp}(r)$, with $ISAR_{exp}(r)$

representing the expectation under the null model. There was strong evidence that *K.*

lanata had more diverse local neighborhoods (at $r < 2$ m) than expected (Fig. 6A, $P <$

0.01). *K. lanata* showed a non constant intensity within the study plot with some gaps in

its distribution (Fig. 4, see chapter 2), but the detection of the accumulator effect under

the heterogeneous null model suggests that habitat association contributes only weakly to

the local accumulation of species richness in *K. lanata* neighborhoods. Repeating the

same analyses without considering the focal species in the calculation of the ISAR curve

revealed no significant departures from the null model (Table 2, Fig. 7). Thus, the

accumulator effect for *K. lanata* was likely the result of its own fine-scale aggregation

(significant at $r < 0.5$ m, see chapter 2) because the nearest conspecific neighbors of *K.*

lanata individuals were on average located closer than expected by the null model.

Similar results were obtained for *A. tridentata* ssp. *wyomingensis*, but the effect of

environment appeared weaker and significantly positive values obtained from the ISAR

analysis occurred at smaller scales ($r < 0.9$ m) with a clear peak at 0.4 m (Fig. 6B). The

GoF test was again highly significant ($P < 0.01$, Table 2). As with *K. lanata*, calculation

of the ISAR curve without the focal species revealed no significant departures from the

null model (Table 2, Fig. 7), thus the accumulator effect for *A. tridentata* ssp.

wyomingensis was likely the result of its own fine-scale aggregation (significant at $r < 0.5$ m; see chapter 2).

There were no significant departures from the null model for *T. canescens* and thus no evidence of the species having more or less diverse local neighborhoods than expected (Fig. 6C, $P > 0.05$). There was weak evidence that both *G. sarothrae* and *A. confertifolia* had more diverse local neighborhoods than expected at $r \approx 0.5$ m (Fig. 6D and Fig. 6E respectively; $P < 0.05$). However, these departures from the null model were not significant as assessed by the GoF test over the 0-4 m interval (Table 2).

Discussion

Traditional univariate and bivariate spatial statistics are commonly used in ecology to investigate plant spatial patterns and to make inferences on ecological processes that structure plant communities (Wiegand and Moloney 2004, Perry et al. 2006, Law et al. 2009). Univariate statistics can describe plant patterns independent of species as well as patterns of individual species, while bivariate statistics may at best describe the patterns of all pairwise species pairs relative to one another. Neither of these approaches considers the distribution of species within a community directly, nor are they sufficient in revealing more complicated plant patterns that are increasingly linked to community-structuring processes. As a result, traditional univariate and bivariate spatial statistics do not effectively summarize diversity patterns at the community level, meaning that critical information related to community structure and species coexistence may fail to be captured (Illian and Burslem 2007, Wiegand et al. 2007a).

This issue is especially relevant in semi-arid shrublands, in which plant aggregations are a common feature (Tirado and Pugnaire 2003, see chapter 2, but see Wiegand et al. 2006) and with few exceptions are most often described in terms of all plants in a study region independent of species (see chapter 2) or in terms of one species relative to another (e.g. Wiegand and Moloney 2004, Perry et al. 2009, see chapter 2). Aggregated plant patterns in semi-arid shrublands have been variously attributed to facilitation (Tirado and Pugnaire 2003, Pugnaire et al. 2011), habitat heterogeneity (Perry et al. 2009), disturbance (Seifan and Kadmon 2006) and localized seed dispersal (Schurr et al. 2004), yet plant aggregations likely encompass more than 1-2 species selected for analysis (e.g. Kéfi et al. 2007, Valiente-Banuet and Verdú 2008).

In this study, analysis of a highly accurate spatial dataset on the species and location of 2,359 shrubs in a semi-arid shrubland revealed significant fine-scale variation in spatial patterns of species diversity. This variation was not captured in a previous analysis of the data using univariate and bivariate spatial statistics, which suggested that the community was characterized by low-diversity or monospecific clusters of individual shrub species (see chapter 2). This conclusion was not supported by our analysis, which showed that the community under study was well-mixed, and that individual shrubs were surrounded by an average of 4.9 shrubs of approximately 2.5 species within neighborhoods of 1 m. Use of the ISAR statistic and appropriate simulation procedures revealed subtle associations of individual species with respect to neighborhood diversity. Local neighborhoods of two species (*K. lanata* and *A. tridentata* ssp. *wyomingensis*) were more diverse than expected by the heterogeneous Poisson null model that accounted for larger-scale environmental effects. The difference between the observed neighborhood

diversity and that expected under the null model was not dramatic (≈ 0.2 species; Fig. 5)

but statistically significant. However, we found that the accumulator effect of these two

species was likely due to intraspecific (but not interspecific) aggregation, i.e., their

nearest conspecific neighbor was located closer than expected by the null model. *A.*

tridentata ssp. *wyomingensis* was the most common shrub species in the study plot (918

individuals, or 39% of all shrubs), while *K. lanata* was the least common (179

individuals, or 8% of all shrubs) (see chapter 2). Fine-scale (<0.5 m) intraspecific

aggregation was detected for both species at fine scales in a previous study of this

community, with the peak of aggregation for *K. lanata* occurring at finer scales than *A.*

tridentata ssp. *wyomingensis* (~0.1 m and ~0.3, m respectively; see chapter 2). For *A.*

tridentata ssp. *wyomingensis*, both its density within the study plot and the fine-scale

nature of its intraspecific aggregation explain the detection of an accumulator effect when

the ISAR analysis was conducted while retaining the focal species. For *K. lanata,* the

initial detection of an accumulator effect was likely caused by the finer-scale nature of its

intraspecific aggregation. Past research suggests the aggregated pattern of *A. tridentata*

ssp. *wyomingensis* we observed could have resulted from local dispersal (Young and

Evans 1989) and/or protection of conspecific seedlings from livestock by mature *A.*

tridentata ssp. *wyomingensis* shrubs (Owens and Norton 1992). Aggregated dispersal

may also partially explain the observed aggregation of *K. lanata* (Booth 2005).

Our analysis suggests that the spatial patterns of the semi-arid shrub community

under study were not characterized by signals from positive plant interactions between

shrub species. This was somewhat surprising, as interspecific facilitation is a common

feature of semi-arid shrublands (Tirado and Pugnaire 2003, Valiente-Banuet and Verdú

2008), especially those characterized by multispecific plant aggregations (Eccles et al. 1999, Kéfi et al. 2007, Valiente-Banuet and Verdú 2008). Similar negative results have been reported by studies on interspecific spatial patterns in tropical forests, savannas, or shrublands (e.g. Wiegand et al. 2006, Lieberman and Lieberman 2007, Wiegand et al. 2007a,b, Perry et al. 2009, Silva et al. 2010, Getzin 2011). On the first view, such results that report absence of expected effects may look uninteresting and insignificant; however, the rise of neutral theories (Hubbell 2001) has turned attention to the absence of interactions as one of the fundamental structural elements of ecological communities of adult plants. Recently, McGill (2010) showed in a synthesis of major theories of biodiversity that all relied on the assertion of absence of species interactions, and that models assuming no spatial interactions have been very successful at making predictions that match empirical data. Results such as ours, reporting absence of strong species interactions, have possibly been suppressed giving the dominant view that species interactions are central to ecology. A considerable challenge of spatial ecology is therefore to provide explanations for balanced spatial structures in plant communities. However, Wiegand et al. (2006) found that the shrub component of a Patagonian shrub-grass steppe was randomly structured. They hypothesized that density-dependent processes such as competition and facilitation may occur mostly at early growth stages of individual shrubs and therefore could not be detected in their spatial analysis. The same argument may hold in this study, since the lack of shrub size-class data precluded analyses of juvenile shrub patterns relative to adults.

Clearly, carefully designed field experiments will be required to confirm the role, if any, that positive plant interactions and other processes play in structuring the

community under study. Our approach may be used in other plant communities to determine if individual species are disproportionately associated with diversity patterns. For example, shrublands occupy much of the Western United States and are subject to management initiatives that seek to better understand processes related to productivity, invasive species, species diversity, and disturbance (e.g. SAGESTEP; http://www.sagestep.org/). The results of this and similar studies may inform management plans that seek to increase and maintain target levels of species diversity, since species that tend to accumulate diversity may become key targets for conservation or restoration efforts.

Conclusion

Recently developed statistics assess spatial patterns of species diversity, allowing for the determination of species-specific associations with neighborhood diversity within a given community. These techniques are especially useful in understanding species dynamics in diverse communities, in which traditional spatial statistics fail to capture the full range of variation in patterns derived from spatial data. We applied one such technique (ISAR) in an analysis of shrub spatial data from a semi-arid shrub community in order to better understand species-specific associations with diversity patterns, and found balanced interspecific patterns instead of the expected positive associations that are expected in semiarid communities. The growing evidence for balanced interspecific patterns of adult members of plant communities represents a challenge for spatial ecology. We anticipate that such approaches will be increasingly used in the future in a

variety of plant communities in order to both describe complex, multispecies spatial patterns and to link patterns to community-structuring processes.

Literature cited

Booth, D. T. 2005. *Krascheninnikovia lanata* (Pursh) A. D. J. Meeuse & Smit. – In: Bonner, F. T. and Nisley, R. G. (eds), *Woody plant seed manual*. U.S. Department of Agriculture, Forest Service, Washington, DC. http://www.nsl.fs.fed.us/wpsm/

Eccles, N. S. *et al*. 1999. Spatial pattern analysis in Namaqualand desert plant communities: evidence for general positive interactions. – Plant Ecol. 142: 71-85.

Getzin, S. *et al*. 2011. Size dominance regulates tree spacing more than competition within height classes in tropical Cameroon. – J. Trop. Ecol. 27: 93-102.

He, F. and Legendre, P. 2002. Species diversity patterns derived from species–area models. – Ecol. 83: 1185-1198.

Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. – Princeton Univ. Press.

Illian, J. B. *et al*. 2008. *Statistical analysis and modeling of spatial point patterns*. – Wiley.

Illian, J. B. and Burslem, D. F. R. P. 2007. Contributions of spatial point process modelling to biodiversity theory. – Journal de la Société Française de Statistique 148: 9–29.

Illian, J. B. *et al*. 2009. Hierarchical spatial point process analysis for a plant community with high biodiversity. – Environ. Ecol. Stat. 16: 389-405.

Kéfi, S. *et al*. 2007. Spatial vegetation patterns and imminent desertification in

    Mediterranean arid ecosystems. – Nature 449: 213-217.

Law, R. *et al*. 2009. Ecological information from spatial patterns of plants: insights from

    point process theory. – J. Ecol. 97: 616-628.

Lieberman, M. and Lieberman, D. 2007. Nearest-neighbor tree species combinations in

    tropical forest: the role of chance, and some consequences of high diversity. –

    Oikos 116: 377-386.

Loosmore, N. B. and Ford, E. D. 2006. Statistical inference using the G or K point

    pattern spatial statistics. – Ecol. 87: 1925-1931.

McGill, B. J. 2010. Towards a unification of unified theories of biodiversity. – Ecol. Lett.

    13: 627-642.

Owens, M. K. and Norton, B. E. 1992. Interactions of grazing and plant protection on

    basin big sagebrush (*Artemisia tridentata* spp. *tridentata*) seedling survival. – J.

    Range Manage. 45: 257-262.

Perry, G. L. W. *et al*. 2006. A comparison of methods for the statistical analysis of spatial

    point patterns in plant ecology. – Plant Ecol. 187: 59-82.

Perry, G. L. W. *et al*. 2009. Nearest-neighbor interactions in species-rich shrublands: the

    roles of abundance, spatial patterns and resources. – Oikos 118: 161-174.

Pugnaire, F. I., Armas C. and Maestre, F. T. 2011. Positive plant interactions in the

    Iberian Southeast: mechanisms, environmental gradients, and ecosystem function.

    – J. Arid Env. doi:10.1016/j.jaridenv.2011.01.016

Schenk, H. J. *et al*. 2003. Spatial ecology of a small desert shrub on adjacent geological

    substrates. – J. Ecol. 91: 383-395.

Schlesinger, W. H. 1990 Biological feedbacks in global desertification. – Science 247: 1043-1048

Schurr, F. M. *et al*. 2004. Spatial pattern formation in semi-arid shrubland: a priori predicted versus observed pattern characteristics. – Plant Ecol. 173: 271-282.

Seifan, M. and Kadmon, R. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a Mediterranean scrub community. – Basic Appl. Ecol. 7: 496-506.

Shimatani, K. 2001. Multivariate point processes and spatial variation of species diversity. – Forestry Ecol. Manage. 142: 215-229.

Shimatani, K. and Kubota, Y. 2004. Quantitative assessment of multispecies spatial pattern with high species diversity. – Ecol. Res. 19: 149-163.

Silva, I. et al. 2010. Herbaceous and shrubby species co-occurrences in Brazilian savannas: the roles of fire and chance. – Community Ecol. 11: 97-104.

Stoyan, D. and Stoyan, H. 1994. *Fractals, random shapes and point fields: methods of geometrical statistics*. – Wiley.

Tirado, R. and Pugnaire, F. I. 2003. Shrub spatial aggregation and consequences for reproductive success. – Oecologia 136: 296-301.

Turkington, R. and Harper, J. L. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I Ordination, pattern and contact. – J. Ecol. 67: 201-218.

Valiente-Banuet, A. and Verdú, M. 2008. Temporal shifts from facilitation to competition occur between closely related taxa. – J. Ecol. 96: 489-494.

Wang, X. *et al*. 2010. Species associations in an old-growth temperate forest in north-eastern China. – J. Ecol. 98: 674–686.

Wiegand, T. *et al*. 2006. Extending point pattern analysis to objects of finite size and
   irregular shape. – J. Ecol. 94: 825-837

Wiegand, T. *et al*. 2007a. How individual species structure diversity in tropical forests. –
   P. Natl Acad. Sci. 104: 19029-19033.

Wiegand, T. *et al*. 2007b. Species associations in a heterogeneous Sri Lankan
   Dipterocarp forest. – Am. Nat. 170: E77-E95.

Wiegand, T. *et al*. 2009. Recruitment in tropical tree species: revealing complex spatial
   patterns. – Am. Nat. 174: E105-E140.

Wiegand, T. and K. A. Moloney. 2004. Rings, circles, and null-models for point pattern
   analysis in ecology. – Oikos 104: 209-229.

Young, J. A. and R. A. Evans. 1989. Dispersal and germination of Big Sagebrush
   (*Artemisia tridentata*) seeds. – Weed Sci. 37: 201-206.

Table 2. Rank of the Goodness-of-Fit (GoF) test for the observed ISAR function with respect to the 199 simulations of the heterogeneous Poisson null model. Ranks > 195 indicate a significant departure from the null model ($P = 0.05$), indicating more diverse plant neighborhoods than expected by chance.

Species	rank GoF test	rank GoF test without focal species
K. lanata	200	145
A. tridentata	200	30
T. canescens	176	8
G. sarothrae	192	163
A. confertifolia	140	47
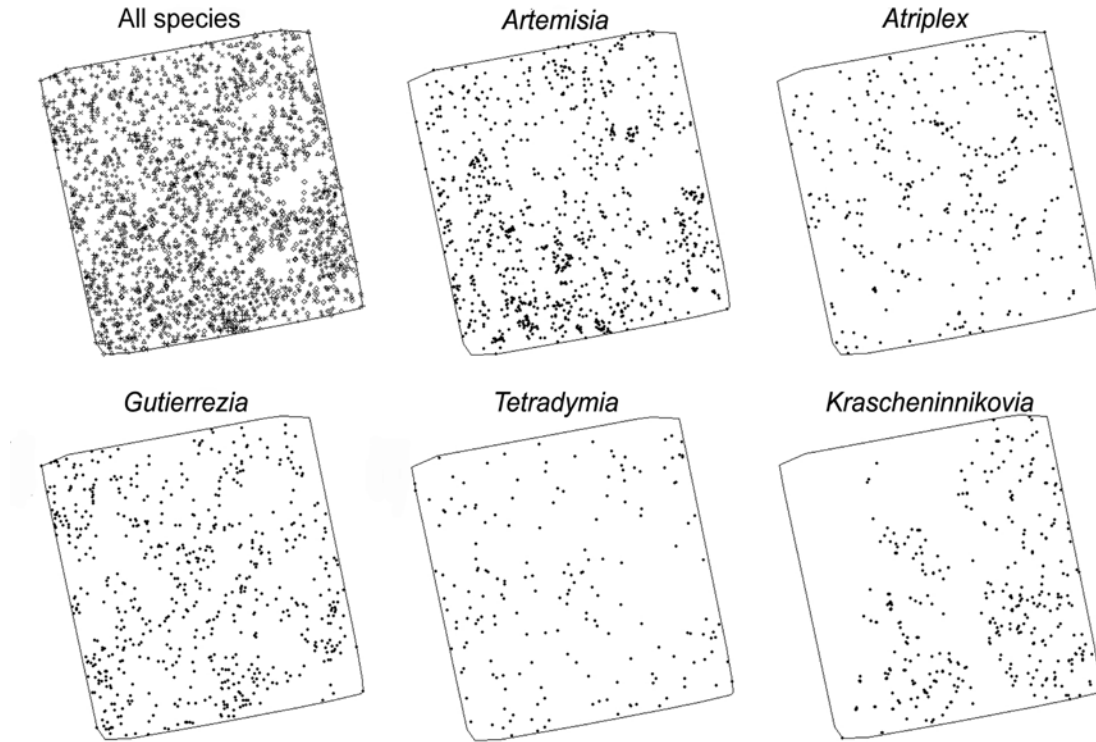
Figure 4. Map of study plot (39m x 39m), showing locations of all shrub individuals (upper left) and maps detailing the locations of individuals from each of the five shrub species. Figure adapted from Rayburn et al. (2011).
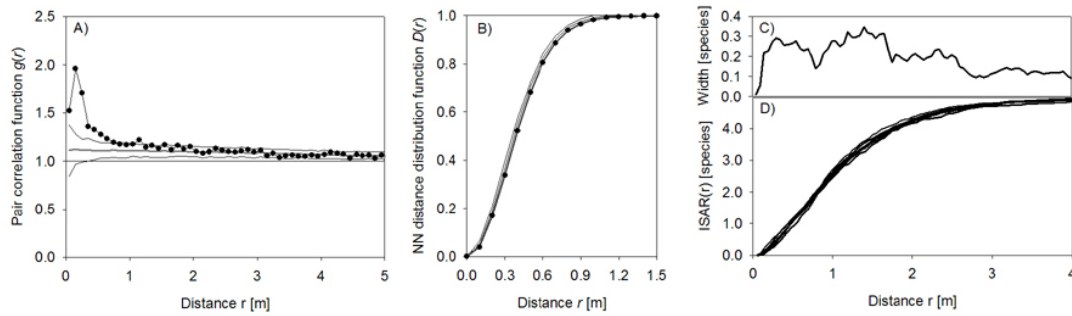
Figure 5. Analysis of the pattern of all shrubs and ISAR functions of individual species. (A) Pair correlation function $g(r)$ of the pattern of all shrubs (dots), simulation envelopes of a heterogeneous Poisson null model with neighborhood R = 4 m (black solid lines) and expectation of the null model (grey line). (B) Distribution functions $D(r)$ of the distances r to the nearest neighbor. Symbols as in A. (C) Maximal difference among individual species area relationships of the five species. (D) Individual species area relationships of the five species (lines; species not labeled).
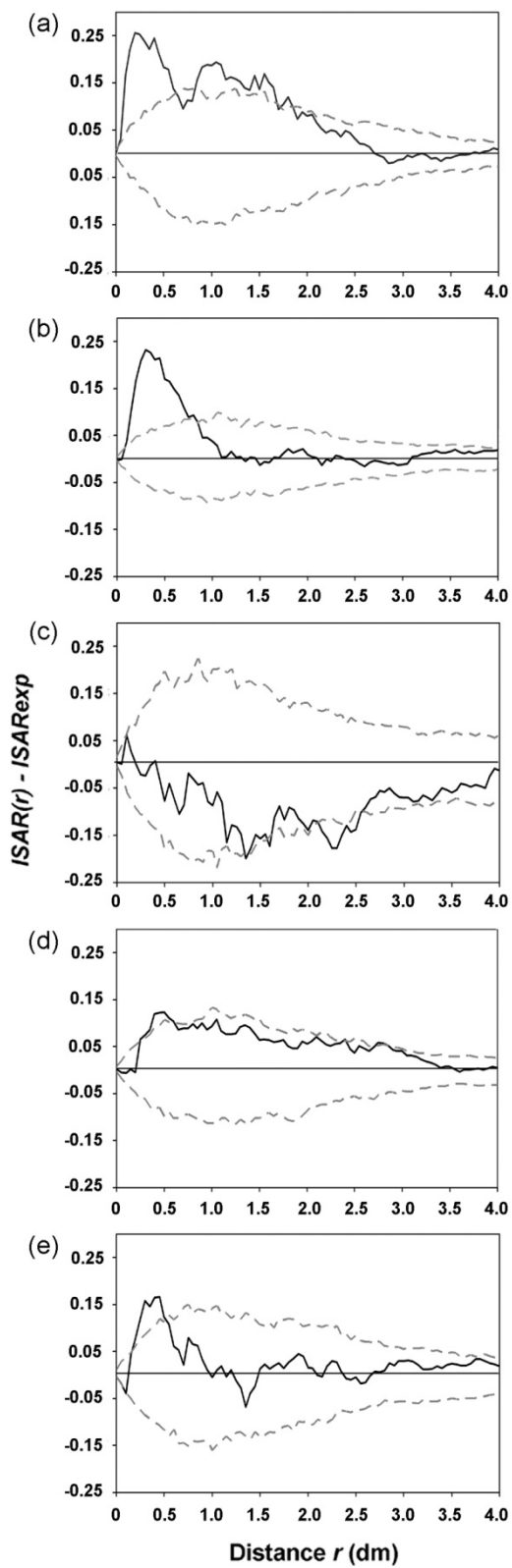
Figure 6. Results of ISAR analyses for (a) *K. lanata*, (b) *A. tridentata* ssp. *wyomingensis*, (c) *T. canescens*, (d) *G. sarothrae*, and (e) *A. confertifolia*. Bold lines show $ISAR_{obs}(r)$-$ISAR_{exp}(r)$, the observed ISAR function minus the expectation of the heterogeneous null model (the average of the ISAR of the 199 null model simulations), grey dashed lines show the simulation envelopes (being the 5th lowest and highest values of the ISAR of the 199 simulations of the null model) minus the expectation of the null model. The ISAR function included the effect of the focal species.
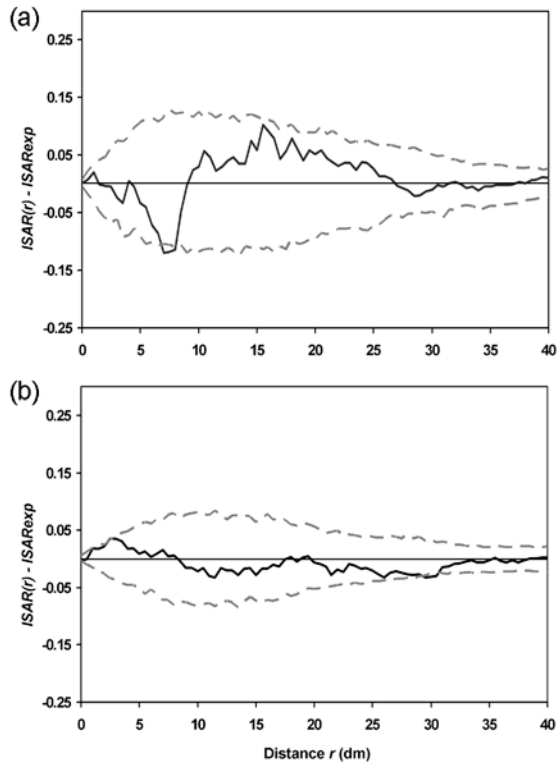
Figure 7. Results of ISAR analyses excluding focal species for (a) *K. lanata* and (b) *A. tridentata* ssp. *wyomingensis*. Bold lines show $ISAR_{obs}(r)$-$ISAR_{exp}(r)$, the observed ISAR function minus the expectation of the heterogeneous Poisson null model (the average of the ISAR of the 199 null model simulations), grey dashed lines show the simulation envelopes (being the 5th lowest and highest values of the ISAR of the 199 simulations of the null model) minus the expectation of the null model.

CHAPTER IV

LINKING PLANT SPATIAL PATTERNS AND ECOLOGICAL PROCESSES IN

GRAZED GREAT BASIN PLANT COMMUNITIES[1] [2]

Abstract

Observational studies of plant spatial patterns are common, but are often criticized for lacking a temporal component and for their inability to disentangle the effect of multiple community-structuring processes on plant spatial patterns. We addressed these criticisms in an observational study of Great Basin (USA) shrub-steppe communities that have been converted to a managed grazing system of planted crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) stands. We hypothesized that intraspecific interference and livestock grazing were important community-structuring processes that would leave unique spatiotemporal signatures. We used a survey-grade GPS to quantify crested wheatgrass spatial patterns along a chronosequence of four stands that differed only in time since planting (9 – 57 yrs), as well as in a 57 yr old grazing exclosure to examine pattern formation in the absence of grazing. Three replicate survey plots were established in each stand, and a total of 6 197 grasses were marked with a spatial error of ≤ 2 cm. The data were analyzed using L-statistics, and hypothesis testing was conducted using Monte Carlo simulation procedures. We detected fine-scale regularity, frequently considered a sign of interference via resource competition, in all stands including the exclosure. Coarser-scale aggregation, which we attributed to the effects of prolonged

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grazing disturbance, was only detected in the oldest grazed stand. Our results suggest that

interference acts over finer spatial and temporal scales than grazing in structuring these

stands, reinforcing the importance of interference in semi-arid communities. Analysis of

exclosure data suggests that, in the absence of grazing, crested wheatgrass stands

organize into a statistically regular pattern when primarily influenced by interference. In

the presence of prolonged grazing, crested wheatgrass stands become more

heterogeneous over time, likely a result of seedling mortality via disturbance by cattle.

Introduction

      Research on plant spatial patterns is often conducted to better understand the

interplay between patterns and ecological processes affecting individual plants and plant

communities (Stoll and Prati 2001; Armas and Pugnaire 2005; Mokany et al. 2008; Law

et al. 2009). Such processes include competitive or facilitative interactions between

individual plants (Kenkel 1988; Stoll and Prati 2001; Murrell 2009), the effect of

environmental heterogeneity on plant survival, growth, and distribution (Tirado and

Pugnaire 2003; Maestre et al. 2003; Schenk et al. 2003), and disturbance (Adler et al.

2001; Bisigato et al. 2005). For example, statistically regular plant spatial patterns are

often assumed to result from intense local competition for limited resources (e.g., Kenkel

1988).

      Observational studies involving snapshot sampling (a single set of observations

without a temporal component) of plant spatial patterns have been frequently conducted

(e.g., Phillips and MacMahon 1981; Skarpe 1991; Schenk et al. 2003). However, attempts

to link the observed patterns to community-structuring ecological processes have been

criticized on the grounds that such studies lack a temporal component and that dynamic ecological processes operate over space and time simultaneously (Lepš 1990; Law et al. 2009). A related criticism is that multiple interacting processes may generate similar plant patterns, and that observational studies of plant pattern formation may be unable to disentangle the effects of multiple processes without additional experimental studies that may be difficult or impossible in the field (McIntire and Fajardo 2009). Recent observational studies of pattern and process have overcome these hurdles by using combinations of *a priori* hypotheses, ecologically informed expectations, and precise spatial analyses that elucidate both the nature of emergent patterns and the scale over which the patterns are detected (e.g., Wiegand et al. 2007; McIntire and Fajardo 2009). However, without a temporal component, there is substantial uncertainty as to the relationship between pattern and process over time (Law et al. 2009).

One potential way to include a temporal dimension in snapshot studies is to study sites that are as similar as possible in environmental and edaphic characteristics, but that vary along a temporal gradient, or chronosequence. If all sites are exposed to the same suite of pattern-forming processes, and if patterns have unique spatial signatures, then a study of sites along the chronosequence may reveal how the processes influence the pattern through time. In this manner, it would be possible to conduct observational studies of plant patterns that nearly equal the power of controlled experiments and which more directly link the observed patterns to community-structuring processes. In this study, we sought to demonstrate this approach across a chronosequence of grazed crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) stands in southeastern Idaho, USA, to examine pattern formation and stand dynamics through time in response to two

ecological processes: intraspecific interference via resource competition and grazing disturbance.

First introduced into the United States from its native range in Russia in 1898 by N. E. Hansen as a promising pasture grass, crested wheatgrass plantings began in the Great Basin region of the western U.S. in the 1930s (Hull and Klomp 1966; Rogler and Lorenz 1983). Crested wheatgrass has many desirable characteristics, such as being a strong competitor against troublesome invasive species such as downy brome (*Bromus tectorum* L.) (Aguirre and Johnson 1991; Chatterton and Harrison 2003), high grazing tolerance (Sharp 1986; Angell 1997), drought tolerance (Caldwell and Richards 1986; Sharp et al. 1992), long life (Hull and Klomp 1966), and high seed production (Marlette and Anderson 1986). To date, millions of hectares of big sagebrush (*Artemisia tridentata* Nutt.)-steppe ecosystems have been seeded with crested wheatgrass in the Great Basin to rehabilitate damaged wildlands and to provide forage within managed grazing systems (Rogler and Lorenz 1983; Pellant and Lysne 2005). Although there is substantial variability across present-day Great Basin crested wheatgrass stands related to soils, time since planting, planting method, land use history, and disturbance history, there are subsets of stands that are very similar in most respects except that they differ in age since planting.

Crested wheatgrass was historically planted in monoculture (Fig. 1), although more recently it has been included in seed mixtures with native grasses and forbs to facilitate more diverse communities (Pellant and Lysne 2005). Although seedling mortality often occurred as a result of poor seedling emergence and survival, grazing (Balph and Malechek 1985; Salihi and Norton 1987), or competition with existing plants

(Hull and Klomp 1967), newly established stands of crested wheatgrass had a distinctly regular pattern similar to agricultural fields.

In years following establishment, these stands were subject to a variety of community structuring processes that may have influenced the spatial pattern of grasses, such as dispersal and seedling establishment and grazing disturbance. For example, Balph and Malechek (1985) reported that cattle avoided walking on the tussocks of established crested wheatgrass plants, preferring instead to move through tussock interspaces. Salihi and Norton (1987) reported extremely high seedling mortality in the same study area, which they attributed to the effects of trampling as cattle moved through interspaces between tussocks, where over 90% of seedlings emerged. In addition to trampling, high levels of grazing may lead to reduced vigor and even mortality of mature crested wheatgrass plants (Pellant and Lysne 2005).

Crested wheatgrass spatial patterns are also likely influenced by intraspecific interference (rather than interspecific interference, as many of the stands have persisted as near-monocultures for decades after establishment; Hull and Klomp 1966; Marlette and Anderson 1986; Kindschy 1991). Interference via resource competition between individual grasses for water and nutrients has been reported for established crested wheatgrass stands and in controlled experiments (Keller and Bleak 1974; Salihi and Norton 1987; Olsen and Richards 1989; Asay and Johnson 1997). For example, Salihi and Norton (1987) found that crested wheatgrass seedlings in both grazed and ungrazed stands most often emerged in bare soil >10 cm from established grasses. The same study found that emergent seedlings that were farther away from established grasses also had the highest rate of survival. Intense intraspecific interference is most likely contributing

strongly to the regularly spaced plant patterns that are a hallmark of certain mature crested wheatgrass stands in the Great Basin (Fig. 8A).

In this study, we sought to quantify long-term changes in grass spatial patterns to better understand how these processes have acted over space and time to structure crested wheatgrass stands in the Great Basin. Evaluating the relationship between plant spatial patterns and community-structuring processes within these stands is timely as managed grazing systems worldwide are challenged with changing bioclimatic, edaphic, and socio-economic pressures (Asner et al. 2004). Our expectations took the form of *a priori* hypotheses as advocated in recent publications regarding appropriate inferences made from observational studies of plant spatial patterns (e.g. McIntire and Fajardo 2009).

Our general hypothesis was that interference and disturbance were important ecological processes determining grass spatial patterns, but that each would leave unique spatiotemporal signatures and act at different spatial scales owing to the specific nature of each process. This hypothesis was based on the assumption that intense intraspecific interference between grasses would likely lead to regularity between crested wheatgrass plants at a scale that reflects the zone of interactions between individual plants, as has been observed in other plant communities structured by competition (e.g., Kenkel 1988). Based on relatively scarce information in the literature, and on our own observations of interplant distances within a grazing exclosure (mean nearest neighbor distance measured between centroids $= 0.17 \pm 0.004$ m, $N = 285$ grasses), we specifically predicted that fine-scale regularity would be detected at a scale of <0.2 m. Conversely, we predicted that disturbance via cattle would be expected to lead to aggregation, at a scale that reflected the movement and grazing patterns of cattle across the stand. As noted above, previous

studies have reported that cattle tended to avoid tussocks of mature crested wheatgrass, and walk instead in the interspaces between grasses. Based on field observations of grass interspaces and cattle movement throughout the study plots, we specifically predicted that aggregation would be detected at a larger scale than regularity (>0.2 m). Relative to the temporal dimension, we predicted that spatial signatures of both processes would be detected in older stands, but that aggregation would not be detected in younger stands owing to a lack of stand development and lack of prolonged grazing disturbance.

Methods

The study stands of crested wheatgrass were located in Oneida Co., southeastern Idaho, USA. Two grazed stands (Bowhuis and South Black Pine) were located within ~2 mi of one another on public land administered by the Bureau of Land Management (US Department of the Interior), as was the grazing exclosure we included in the study to control for the effects of grazing on pattern formation. The third grazed stand (North Carter) was located ~14.5 mi away within Curlew National Grasslands, which is administered by the Forest Service (US Department of Agriculture).

Prior to plot establishment, the age of each stand was determined either from previous published work (Williams 2009) or from interviews with local management agency staff. Stands varied in time since planting (9, 37, and 57 yrs) but were similar in terms of site preparation prior to planting, planting method, disturbance history, and Ecological Site descriptions (ESDs; USDA 2010) (Table 3). In addition, ESDs indicate that all four stands historically supported Wyoming big sagebrush- bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) plant communities. Replicate stands were not

available in the region, since many stands had previously burned and/or had been

established and managed using different methods. The exact grazing history for each

stand was difficult to determine; however, all grazed stands in the study have experienced

high stocking rates and intensive grazing annually since their establishment (Williams

2009). The stand in which the exclosure was located was planted at the same time as the

South Black Pine stand, while the grazing exclosure itself was constructed approximately

40 yrs ago. The inclusion of additional, younger exclosures in the study would have been

preferable; however, no other exclosures existed in the region. While domestic cattle and

sheep were not permitted into the exclosure, wildlife could freely enter by leaping the

fence or through gaps in the fence. None of the study stands have experienced fire since

they were seeded with crested wheatgrass. Stands were characterized by flat topography,

uniformity in vegetation height, and little to no woody vegetation.

Three 5 m x 5 m plots were established in each grazed stand, as well as in the

exclosure. Within each plot, all perennial vegetation was identified and mapped using the

ProMark3 GPS system, a survey-grade GPS unit that enables both rapid and precise data

collection (see chapter 2). GPS data were collected at the approximate centroids of each

plant. Plots were essentially monocultures, with no other perennial or woody species

present and only scattered annual vegetation.

Field GPS data was post-processed using GNSS Solutions software (v. 3.10.01,

Magellan Navigation), and the resulting *x,y* coordinates of plants had an estimated spatial

error of ≤ 2 cm. Coordinates were exported for statistical analysis in R (v. 2.10.0, R

Development Core Team) using both base functions and the *spatstat* package for spatial

analysis of point patterns (v. 1.14.7, Baddeley and Turner). We calculated the common

second-order spatial statistic Ripley's K (Ripley 1981), which evaluates the number of

points within a certain distance (r) of a randomly chosen point relative to expectations

based on the density of points in the study area The approximately unbiased estimator

for $K(r)$ is

$$\hat{K}(r) = n^{-2}A\sum\sum w_{ij}^{-1}I_r(u_{ij})$$

(1)

where n is the number of plants in the study plot, A is plot area, I_r is a counter variable,

u_{ij} is the distance between events i and j, and w_{ij} is a weighting factor to correct for edge

effects (Haase 1995). A variety of null models and edge corrections may be implemented

for K-statistics, depending on the nature of the analysis. Significant deviations of the K-

statistic indicate either regularity or aggregation at scale r in a spatial point pattern

dataset, assuming an appropriate null model has been fit. K-statistics are often square-

root transformed $(L(r) = \sqrt{[K(r)/\pi]}$ following Besag 1977) to stabilize variance, and

plotted using $(L(r) - r)$ against r since this derived function has an expectation of 0 for all

values of r under the null hypothesis of complete spatial randomness (CSR) (Skarpe

1991).

We evaluated the crested wheatgrass spatial data using a CSR null model coupled

with reduced sample edge correction and Monte Carlo permutation procedures

(N_{sim}=199) for hypothesis testing. The CSR null model was appropriate as there were no

obvious first-order effects influencing patterns of crested wheatgrass.

Results

A total of 6 197 grasses were mapped across the twelve study plots. Grass densities varied from 7.1 grasses/m^2 to 34.3 grasses/m^2, and densities were generally higher in the older grazed plots versus the young grazed plots and the exclosure plots (Table 3). Significant fine-scale ($r < 0.2$ m) regularity was detected in all nine grazed study plots (Fig. 9A-I), with broader-scale (r > 0.6 m) regularity detected in one of the 9 yr old study plots (Fig. 9E). Significant fine-scale regularity was also detected in all three exclosure plots (Fig. 9J-L), albeit across a broader scale in two of the three plots ($r \approx 0.0$ – 0.8 m and $r \approx 0.0 - 0.6$ m; Fig. 9J & L). Significant aggregation was only detected in the older grazed plots. In two plots within the oldest stand, significant aggregation was detected at broader scales than regularity ($r \approx 0.1 - 0.4$ m and $r \approx 0.1 - 0.8$ m; Fig. 9H & I). There was also suggestive evidence of significant aggregation in two plots within the intermediate-aged stand ($r \approx 0.2$ m and $r \approx 0.2$ m; Fig. 9E & F). By suggestive, we mean that the values of the L-statistic were extremely close to the values of the null model, and that results should be interpreted with caution (Blanco et al. 2008).

Discussion

Observational studies of plant spatial patterns are common, but have been criticized on the grounds that they lack the power of experimental studies for connecting pattern and process in plant communities. Ideally, one would conduct a complete spatiotemporal experiment in which the type and magnitude of ecological processes were known and in which established plots or study regions were monitored over a sufficiently long period of time to track population data in addition to changes in plant spatial

patterns. Examples of these kinds of studies are rare, however, owing in no small part to the difficulties in establishing such experiments, and have tended to focus on the effects of aggregation on species coexistence (Stoll and Prati 2001; Monzeglio and Stoll 2005; Mokany et al. 2008).

In this study, we sought to address past criticisms of observational studies by using an approach designed to disentangle the long-term effects of grazing disturbance and intraspecific interference via resource competition on plant patterns in grazed Great Basin crested wheatgrass stands. We hypothesized that competition would rapidly lead to fine-scale regularity between individual grasses, while grazing would likely lead to aggregation at coarser spatiotemporal scales. Our GPS-based approach allowed us to precisely quantify grass spatial patterns, allowing us to test for unique spatial signatures of grazing and competition using second-order spatial statistics. By collecting spatial data on grass patterns across a chronosequence of similar stands, we enhanced our understanding of the temporal scales at which the processes under study act to structure the community. We suggest that this methodology could be useful in other community types where multiple ecological processes are under study and long-term field experiments are not tractable.

Our results strongly suggest that crested wheatgrass stands are simultaneously structured by both interference and grazing, albeit at different spatiotemporal scales. At fine spatial scales, we detected significant regularity between individual plants in all plots, which we attribute to strong local competitive interactions for water and nutrients. This regularity is likely not simply a relict of the initial pattern of planting; as substantial rearrangement (relative to linear rows) of crested wheatgrass plants was apparent in even

the youngest plots. Previous studies have found that crested wheatgrass stands could quickly thicken and spread relative to the initial pattern of planting (Weintraub 1953; Hull and Klomp 1966; Hull and Klomp 1967), likely due to high levels of seed production in crested wheatgrass (Marlette and Anderson 1986) coupled with interspaces between planted rows that provided room for seedling establishment. As space for new recruits became more limited, it is likely that intraspecific competition for resources quickly became an important community structuring process. Competition is likely more intense in the exclosure, as evidenced by the detection of regularity across broader scales in exclosure plots as compared to grazed plots.

At coarser spatial scales, we detected significant aggregation in two of the three oldest crested wheatgrass plots examined, which we attribute to the effects of sustained disturbance by cattle. Grazing disturbance can have profound effects on the spatial pattern of vegetation (Adler et al. 2001; Adler and Hall 2005; Henkin et al. 2007). Depending on the characteristics of species being grazed, grazing intensity, and on the other biotic and abiotic characteristics of the community, grazing is known to influence the spatial structure of the grazed species (Seifan and Kadmon 2006), plant interactions within the community (Murrell et al. 2001), biomass production (Seifan and Kadmon 2006), and plant mortality (Salihi and Norton 1987; Huntly 1991).

In our study, the observed aggregation in the oldest stand was likely the result of decades of cattle moving through interspaces between established crested wheatgrass tussocks, leading to increased seedling mortality in the interspaces as observed in past studies of grazed crested wheatgrass stands (Balph and Malechek 1985; Salihi and Norton 1987). This effect is exacerbated in older stands, as crested wheatgrass tussocks

become more elevated relative to the surrounding substrate (Balph and Malechek 1985).

In young stands without significant tussock development, cattle are likely to step more

randomly throughout the stand; as tussocks form, cattle are more likely to step in the

interspaces to avoid the uneven terrain associated with the tussocks. These interspaces

undergo additional soil compaction, resulting in a positive feedback mechanism as soil

compaction increases the elevation of surrounding tussocks, which in turn increases non-

random movement of cattle through the stand (Balph and Malechek 1985) and

subsequent aggregation. The creation of cattle trails in crested wheatgrass stands

represents the extreme case of the above scenario, as soil is very compacted on trails and

few if any seedlings are present. In the absence of trails, however, significant patchiness

may form in crested wheatgrass stands as a result of non-random movement of cattle and

subsequent grazing, trampling, and soil compaction (Fig. 8B).

Implications

Grazing disturbance and interference both appear to shape spatial patterns of

crested wheatgrass stands in the northeastern Great Basin, USA. Understanding how

these important ecological processes operate through time provides new insight into how

land users or managers can assess site conditions and develop strategies to trigger

desirable vegetation changes. Our results suggest measurements of plant spatial patterns

could augment rangeland-monitoring programs, which typically only measure plant cover

or density. For example, assessment of plant spatial patterns may assist contemporary

efforts to diversify crested wheatgrass communities (Cox and Anderson 2004; Pellant and

Lysne 2005). In this context, identifying spatial patterns should better inform managers

who need to better predict competitive interactions between plants when reducing crested wheatgrass dominance with mechanical and chemical methods. Thus, rapid recovery of crested wheatgrass from seed banks within 2–3 yrs after reduction treatments (Hulet et al. 2010) and differential interference between crested wheatgrass and native species as seedlings (Gunnell et al. 2010) may depend not only on the specific management approach employed, but also on how grazing and interference affect site-specific plant spatial patterns.

Our observation of significant fine-scale regularity between individual plants in all plots confirms that interference interactions for water and nutrients are intense in crested wheatgrass stands. In the absence of grazing, interference intensity likely increases as regularity persisted across broader scales in exclosure plots as compared to grazed plots. Our results also indicated that sustained disturbance by cattle in older stands creates significant aggregation, albeit at broader scales than regular patterns caused by interference.

Literature cited

Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128:465-479.

Adler, P. B., and S. A. Hall. 2005. The development of forage production and utilization gradients around livestock watering points. *Landscape Ecology* 20:319-333.

Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *Journal of Range Management* 44:347-354.

Angell, R. A. 1997. Crested wheatgrass and shrub response to continuous or rotational grazing. *Journal of Range Management* 50:160-164.

Armas, C., and F. I. Pugnaire. 2005. Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology* 93:978-989.

Asay, K. H., and D. A. Johnson. 1997. Genotype x competition level interactions in crested wheatgrass (Agropyron desertorum Poaceae: Triticeae). *International Journal of Plant Sciences* 158:851-855.

Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* 29:261-299.

Balph, D. F., and J. C. Malechek. 1985. Cattle trampling of crested wheatgrass under short-duration grazing. *Journal of Range Management* 38:226-227.

Besag, J. 1977. Contribution to the discussion of Dr. Ripleys paper. *Journal of the Royal Statistical Society* B25:294.

Bisigato, A. J., M. B. Bertiller, J. O. Ares, and G. E. Pazos. 2005. Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. *Ecography* 28:561-572.

Blanco, P. D., C. M. Rostagno, H. F. del Valle, A. M. Beeskow, and T. Wiegand. 2008. Grazing impacts in vegetated dune fields: predictions from spatial pattern analysis. *Rangeland Ecology and Management* 61:194-203.

Caldwell, M. M., and H. Richards. 1986. Ecophsiology of crested wheatgrass: a comparative study with bluebunch wheatgrass. *In*: K. L. Johnson [ED.]. Crested wheatgrass: its values, problems, and myths. Symposium proceedings. Utah State University, Logan, UT, USA: p. 165-167.

Chatterton, H. J., and P. A. Harrison. 2003. Fructans in crested wheatgrass leaves. *Journal of Plant Physiology* 160:843-849.

Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management* 57:203-210.

Gunnell, K. L., T. A. Monaco, C. A. Call, and C. V. Ransom. 2010. Seedling interference and niche differentiation between crested wheatgrass and contrasting native Great Basin species. *Rangeland Ecology and Management* 63:443-449.

Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. *Journal of Vegetation Science* 6:575-582.

Henkin, Z., L. Hadar, and E. Noy-Meir. 2007. Human-scale structural heterogeneity induced by grazing in a Mediterranean woodland landscape. *Landscape Ecology* 22:577-587.

Hulet, A., B. A. Roundy, and B. Jessop. 2010. Crested wheatgrass control and native plant establishment in Utah. *Rangeland Ecology and Management* 63:450-460.

Hull, A. C., Jr., and G. J. Klomp.1966. Longevity of crested wheatgrass in the sagebrush-grass type in southern Idaho. *Journal of Range Management* 19:5-11.

Hull, A. C., Jr., and G. J. Klomp. 1967. Thickening and spread of crested wheatgrass stands on southern Idaho ranges. *Journal of Range Management* 20:222-227.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22:477-503.

Keller, W., and A. T. Bleak. 1974. Growth and seed production of Nordan crested

wheatgrass in a modified corn wheel. *Crop Science* 14:115-117.

Kenkel, N. C. 1988. Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. *Ecology* 69:1017-1024.

Kindschy, R. R. 1991. Alfalfa in crested wheatgrass seedings. *Rangelands* 13:244-246.

Law, R., J. Illian, D. F. R. P. Burslem, G. Gratzer, C. V. S. Gunatilleke, and I. A. U. N. Gunatilleke. 2009. Ecological information from spatial patterns of the plants: insights from point process theory. *Journal of Ecology* 97:616-628.

Lepš, J. 1990. Can underlying mechanisms be deduced from observed patterns? *In* F. Krahulec et al. [EDS.]. Spatial processes in plant communities. Prague, Academia. p. 178-196.

Maestre, F. R., J. Cortina, S. Bautista, J. Bellot, and R. Vallejo. 2003. Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. *Ecosystems* 6:630-643.

Marlette, G. M., and J. E. Anderson. 1986. Seed banks and propagule dispersal in crested wheatgrass stands. *Journal of Applied Ecology* 23:161-175.

McIntire, E. J. B., and A. Fajardo. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90:46-56.

Mokany, K., J. Ash, and S. Roxburgh. 2008. Effects of spatial aggregation on competition, complementarity, and resource use. *Austral Ecology* 33:261-270.

Monzeglio, U., and P. Stoll. 2005. Spatial patterns and species performance in experimental plant communities. *Oecologia* 145:619-628.

Murrell, D. J. 2009. On the emergent spatial structure of size-structured populations: when does self-thinning lead to a reduction in clustering? *Journal of Ecology*

97:256-266.

Murrell, D. J., D. W. Purves, and R. Law. 2001. Uniting pattern and process in plant ecology. *Trends in Ecology and Evolution* 16:529-530.

Olson, B. E., and J. H. Richards. 1989. Crested wheatgrass growth and replacement following fertilization, thinning, and neighbor plant removal. *Journal of Range Management* 42:93-97.

Pellant, M., and C. R. Lysne. 2005. Strategies to enhance plant structure and diversity in crested wheatgrass seedings. US Department of Agriculture, Forest Service Proceedings RMRS-P-38. p. 16-33.

Phillips, D. L., and J. A. MacMahon. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecol*ogy 69:97-115.

Ripley, B. D. 1981. Spatial processes. New York, NY, USA: Wiley.

Rogler, G. A., and R. J. Lorenz. 1983. Crested wheatgrass – early history in the United States. *Journal of Range Management* 36:91–93.

Salihi, D. O., and B. E. Norton. 1987. Survival of perennial grass seedlings under intensive grazing in semi-arid rangelands. *Journal of Applied Ecology* 24:145-151.

Schenk, H. J., C. Holzapfel, J. G. Hamilton, and B. E. Mahall. 2003. Spatial ecology of a small desert shrub on adjacent geological substrates. *Journal of Ecology* 91:383-395.

Seifan, M., and R. Kadmon. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a Mediterranean scrub community. *Basic and Applied Ecology* 7:496-506.

Sharp, L. A. 1986. Crested wheatgrass: its values, problems and myths. *In*: K. L. Johnson [ED.]. Crested wheatgrass: its values, problems, and myths. Symposium proceedings. Utah State University, Logan, UT, USA: p. 3-6.

Sharp, L. A., K. Sanders, and N. Rimbey. 1992. Variability of crested wheatgrass production over 35-years. *Rangelands* 14:153-168.

Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science* 2:565-572.

Stoll, P., and D. Prati. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82:319-327.

Tirado, R., and F. I. Pugnaire. 2003. Shrub spatial aggregation and consequences for reproductive success. *Oecologia* 136:296-301.

USDA, NRCS. 2010. Ecological Site information system. Available at: http://esis.sc.egov.usda.gov/. Accessed 3 August 2010.

Weintraub, F. 1953. Grasses introduced into the United States. Washington, D.C., USA: US Department of Agriculture, Handbook 58. 79 p.

Wiegand, T., C. V. S. Gunatilleke, I. A. U. N. Gunatilleke, and A. Huth. 2007. How individual species structure diversity in tropical forests. *Proceedings of the National Academy of Science* 104:19029-19033.

Williams, J.R. 2009. Vegetation characteristics of Wyoming big sagebrush communities historically seeded with crested wheatgrass in Northeastern Great Basin, USA [thesis]. Logan, UT, USA: Utah State University. 99 p.

Table 3. Characteristics of the four crested wheatgrass study stands measured in 25 m^2 plots. All stands had identical pre-seeding treatments (plowing), seeding methods (drill), and post-seeding treatments (none). Three sites (Bowhuis, South Black Pine, Exclosure) share identical Ecological Site descriptions (ESD code R028AY024ID), while the ESD for the remaining site (North Carter) has potentially greater annual precipitation and coarser soils (ESD code R028AY025ID).

Stand	Plot	Density (plants/m^2)	Stand age (years)	Mean annual ppt. (mm)	Soil texture	Disturbance history
North Carter			9	280 – 330	Gravelly silt loam	Grazed yearly
	1	16.4				
	2	18.1				
	3	7.1				
Bowhuis			37	203 – 355	Silt loam	Grazed yearly
	1	33.4				
	2	29.2				
	3	34.3				
South Black Pine			57	203 – 355	Silt loam	Grazed yearly
	1	25.8				
	2	16.4				
	3	30.0				
Exclosure			57	203 – 355	Silt loam	Ungrazed
	1	11.4				
	2	14.6				
	3	11.2				
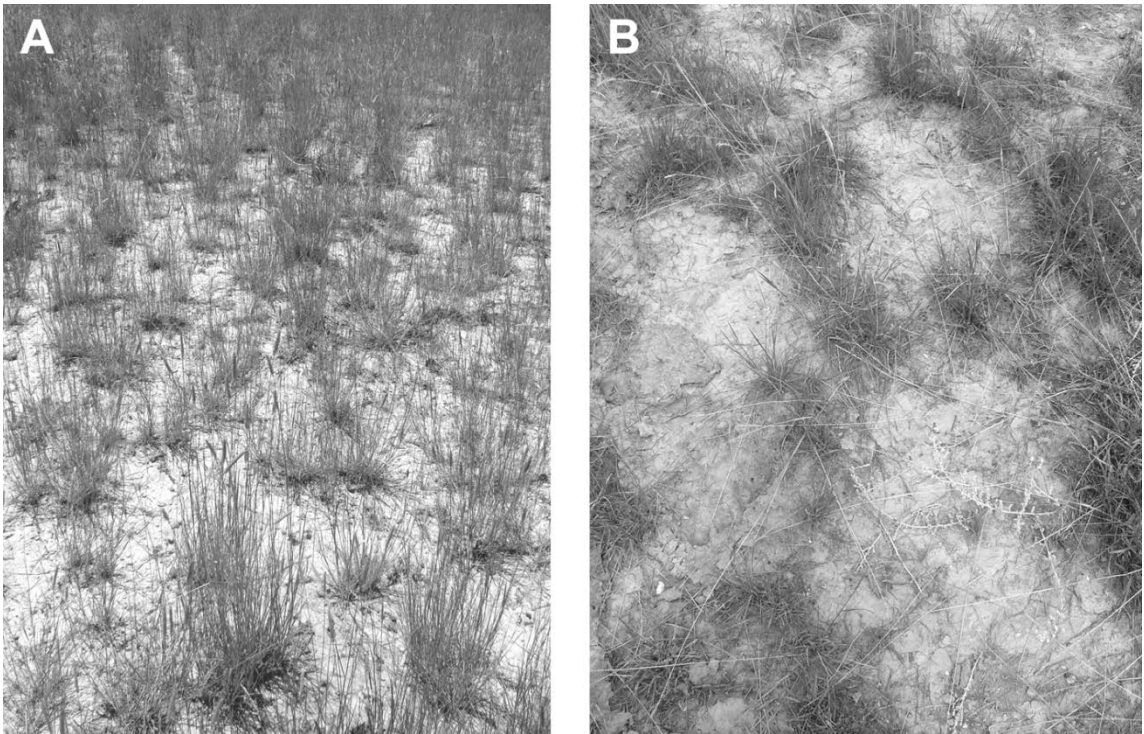
Figure 8. 2010 photographs of 57 yr old crested wheatgrass stand in Oneida County, ID; (**A**) visually regular pattern associated with mature, ungrazed stand, and (**B**) example of aggregation in grass distribution within an adjacent, grazed stand. Photographs by A. Rayburn.
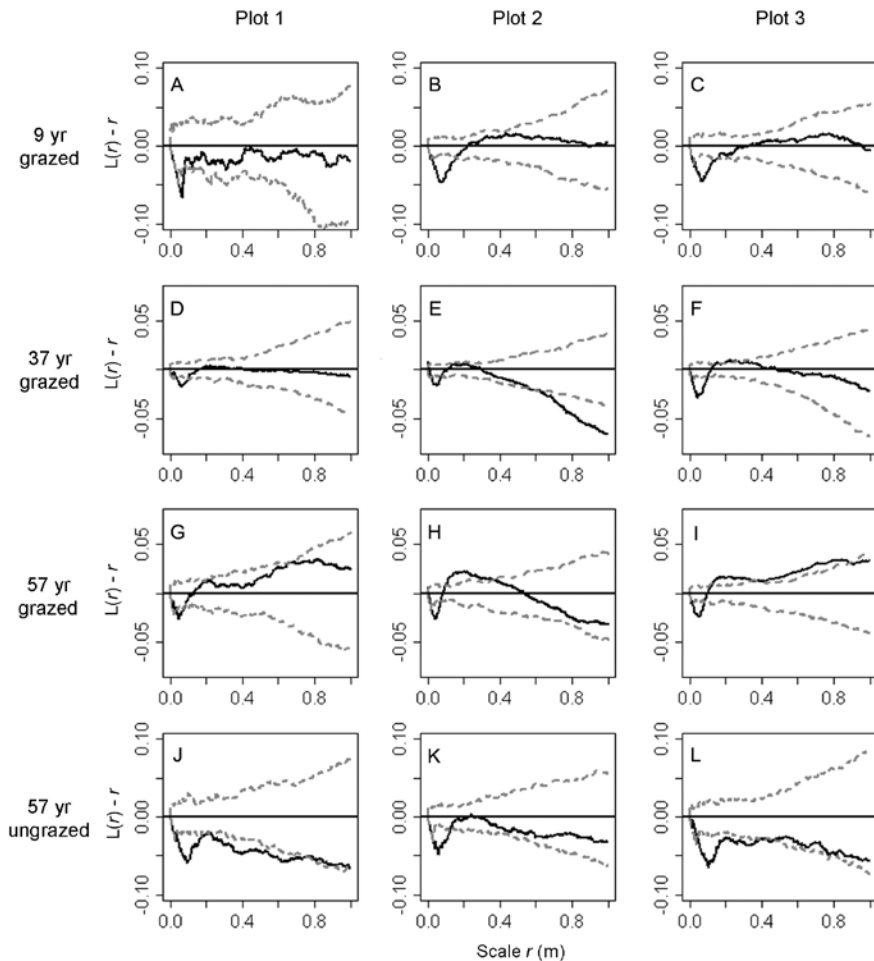
Figure 9. L-function plots for **(A-C)** North Carter (9 yr grazed), **(D-F)** Bowhuis (37 yr grazed), **(G-I)** South Black Pine (57 yr grazed), and (**J-L**) Exclosure (57 yr grazed). Solid lines represent the estimated L-statistics plotted as ($L(r) - r$). Dotted lines represent Monte Carlo simulation envelopes (N_{sim}=199). Values of ($L(r) - r$) greater than the upper simulation envelope indicate significant aggregation relative to the null hypothesis of complete spatial randomness (e.g. plot **H**), while values less than the lower simulation envelope indicate significant regularity (e.g. plot **A**). Horizontal axis values represent the scale (r, in meters) over which the pattern was tested. Plots are not displayed at $r > 1.0$ m because plants are assumed to interact only at fine-scales ($r < 1.0$ m).

CHAPTER V

PLANT SPATIAL PATTERNS AFFECT COMMUNITY DYNAMICS

IN EXPERIMENTAL SEMI-ARID PERENNIAL

GRASSLAND COMMUNITIES

Abstract

A central goal of plant ecology is to elucidate the processes that structure plant communities in space and time. Plant spatial patterns are known to influence community-structuring processes, yet few empirical studies have directly addressed the effects of these factors on community dynamics using realistic experimental communities. Our objective was to test the effects of both community- and neighborhood-scale plant spatial patterns on biotic and abiotic components of experimental semi-arid grassland communities. We manipulated spatial patterns of two co-occurring semiarid perennial grasses: a common cultivar of the strongly competitive crested wheatgrass (*Agropyron cristatum*) and Snake River wheatgrass (*Elymus wawawaiensis*), a relatively weaker competitor. Treatments consisted of interspecific mixtures of the two species in 12 combinations of community-scale spatial patterns (regular, random, and two types of aggregation) and neighborhood-scale aggregation (no aggregations, small aggregations, and large aggregations). Patterns were generated using spatial simulation software, and precisely replicated in the field to produce realistic experimental communities. Two years of data were collected on above-ground production and relative growth rates of approximately 2000 grasses. Variability in light (PAR) and soil moisture were also quantified. There were significant main effects of *treatment* and *year* on mean biomass

independent of species and for both species individually. There were also significant

effects of *treatment* on relative growth rates for both species in 2009. Mean biomass and

mean RGR of both species were highest in plots with community-scale regularity and no

neighborhood-scale aggregation, suggesting a strong effect of interspecific competition

that was magnified for the weaker competitor *E. wawawaiensis* especially in the second

year. Lastly, there were significant effects of *treatment* and *year* on the variability of both

PAR and soil moisture, suggesting that plant spatial patterns influence the heterogeneity

of key plant resources at a community-scale. In the case of PAR, more heterogeneous

light environments were observed in more aggregated treatments, and variability in both

PAR and soil moisture was greater in the second study year. Our research represents one

of the largest manipulative field studies testing the effects of plant spatial patterns, and

provides new information on the role of plant patterns in structuring semi-arid plant

communities.

Introduction

Of the numerous factors that influence the dynamics of plant communities in

space and time, spatial patterns of vegetation have significant effects on plant growth,

interactions, survival and reproduction as well as the distribution of limited abiotic

resources (Stoll and Prati 2001; Valladares 2003; Perry et al. 2009). Plant spatial patterns

in many natural communities are often non-random, being either over-dispersed (regular)

or aggregated to some degree at one or more spatial scales (Stoll and Prati 2001; Maestre

et al. 2005; see chapter 2). Patterns may be scale-dependent; for example, plants may be

aggregated at relatively broad scales within a community (Klausmeier 1999; Wiegand et

al. 2007; see chapter 2), yet fine-scale plant neighborhoods within the same community may be characterized by other non-random patterns (Lortie et al. 2005; Wiegand et al. 2007; see chapter 2). Aggregated patterns are especially common in arid and semi-arid communities (Went 1942; Sala and Aguiar 1996; Rayburn et al. 2011) due to factors such as positive plant interactions (Haase et al. 1996; Valiente-Banuet and Verdú 2008), disturbance (Seifan and Kadmon 2006; see chapter 4), seed dispersal (Schurr et al. 2004), and habitat heterogeneity (Tirado and Pugnaire 2003; Perry et al. 2008; Perry et al. 2009). Statistically regular patterns have also been observed in water-limited plant communities (Phillips and MacMahon 1981; Skarpe 1991; see chapter 4) and are often interpreted as the result of intense intra- or interspecific competition for soil moisture and nutrients (Kenkel 1998; Stoll and Bergius 2005; Rayburn and Monaco 2011).

There is an extensive history of research on the formation of plant spatial patterns (e.g. Haase et al. 1996; Tirado and Pugnaire 2003; Rayburn and Monaco 2011). Less common are studies of the effects of plant spatial structure on population and community dynamics (Tilman and Kareiva 1997; Murrell et al. 2001; Stoll and Prati 2001; Dunstan and Johnson 2003; Maestre et al. 2005; Turnbull et al. 2007). Plants interact almost exclusively with local neighbors (Harper et al. 1997), so the fine-scale spatial patterns of plants in local neighborhoods may in large part determine the direction and magnitude of plant interactions (Pacala 1997; De Boeck et al. 2006; Turnbull et al. 2007) and potentially species coexistence (Stoll and Prati 2001; Murrell and Law 2003; Monzeglio and Stoll 2005). Numerous theoretical studies have tested the prediction that spatial structure impacts plant populations and communities (e.g. Czárán and Bartha 1992; Pacala and Deutschman 1995; Bolker et al. 2003; De Boeck et al. 2006; Turnbull et al.

2007). In addition, many observational studies have sought to link plant spatial patterns
to plant community and population dynamics (e.g. Schurr et al. 2004, Fajardo and
McIntire 2007; Rayburn and Monaco 2011). Empirical tests of the effects of plant spatial
patterns were formerly rare (Tilman and Kareiva 1997; Stoll and Prati 2001; Dunstan and
Johnson 2003), but have increased in number within the last decade (e.g. Stoll and Prati
2001; Tirado and Pugnaire 2003; Monzeglio and Stoll 2005; Turnbull et al. 2007;
Mokany et al. 2008; Lamošová et al. 2010).

General conclusions emerging from these manipulative experiments have
supported predictions from theoretical and observational research: non-random spatial
structure may critically influence many aspects of community and population dynamics.
However, substantial work remains to understand the effects of plant spatial patterns in
realistic communities (Turnbull et al. 2007), especially since many past manipulative
experiments have focused on annual vegetation over short time scales (e.g. Stoll and Prati
2001; Monzeglio and Stoll 2005; Turnbull et al. 2007). Perennial grasses comprise a
substantial portion of terrestrial vegetation, especially in arid and semi-arid regions
(Daubenmire 1970; West et al. 1979; West 1983; West 1988; Pellant and Lysne 2005;
Jones 2008). The effects of grass spatial patterns on plant interactions, recruitment,
mortality, invasion, and production in these communities are still poorly understood,
although some progress has recently been made (e.g. Mokany et al 2008; Lamošová et al.
2010).

While vegetation patterns influence a range of biotic processes in plant
communities, they also influence the fine-scale heterogeneity of key abiotic resources
such as soil nutrients (Schlesinger et al. 1996), soil moisture (Bhark and Small 2003;

Cantón et al. 2004; Bhark and Small 2003), and light (Martens et al. 2000; Valladares

2003; Mokany et al. 2008). However, studies that manipulate plant spatial patterns are

somewhat rare (see above) and rarer still are studies that assess the effect of plant spatial

patterns on abiotic resources such as light and soil moisture (Bolker et al. 2003, but see

Martens et al. 2000 and Maestre et al. 2005). As a result, there is still substantial

uncertainly as to the specific effects of plant spatial patterns on environmental

heterogeneity in both space and time.

In water-limited plant communities, soil moisture may be a critical resource

whose spatiotemporal distribution significantly affects community structure and

dynamics (Harper 1977, Rodriguez-Iturbe et al. 1999; Cantón et al. 2004). For example,

fine-scale heterogeneity in soil moisture distribution almost certainly influences

competitive interactions between plants in water-limited communities with similar

strategies for obtaining soil moisture (Pacala and Tilman 1994; Rodriguez-Iturbe et al.

1999). The spatial pattern of plants in a community may influence the distribution of soil

moisture via direct and indirect pathways, including patterns of infiltration (Bhark and

Small 2003) and plant water use (Mokany et al. 2008).

Another potentially limiting resource is light, which provides the energy used by

plants in photosynthesis and signals used in photoregulation of plant growth and

development (Valladares 2003). In more arid environments, there is usually plentiful or

excess PAR at the canopy due to photosynthetic limitations imposed by water stress

(Martens et al. 2000; Valladares 2003). Light may still be limiting, however, in the

understory beneath arid or semi-arid vegetation and may exhibit significant fine-scale

heterogeneity (Breshears et al. 1997, 1998; Martens et al. 2000). In more arid

communities, the distribution of understory light is especially important in influencing microhabitat variables (e.g. soil and leaf temperatures, soil moisture and evaporation) that significantly affect a range of plant processes such as seedling establishment, germination, plant growth, and plant interactions (Martens et al. 1997; Martens et al. 2000; Valladares 2003). Plant spatial patterns are especially important determinants of understory light distributions near ground level (e.g. Mokany et al. 2008), and striking differences in microhabitat variables are often observed over very small spatial scales such as adjacent canopy and intercanopy patches (Schlesinger et al. 1996; Breshears et al. 1997; 1998).

In this study, our goal was to test the effects of plant spatial patterns on both biotic and abiotic aspects of semi-arid community dynamics using realistic experimental communities comprised of mixtures of two cool-season (C3) Great Basin perennial bunchgrasses, a cultivar of the introduced crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and the native Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth). Our specific objectives were to test the effect of community- and neighborhood-scale patterns on (1) above-ground biomass production (independent of species and for each species individually) and relative growth rates (for each species individually), and (2) variability of both light (photosynthetically active radiation; PAR) near ground-level and soil moisture in the upper 10 cm of the soil. We hypothesized that both biomass and RGR would be higher in plots regularly-spaced at the community-scale with random neighborhoods. We also hypothesized that community-scale biomass and RGR would be significantly reduced in the second year, especially for the presumably weaker competitor *E. wawawaiensis*. Conversely, we hypothesized that both light and

soil moisture would be more heterogeneous in plots with community-scale aggregation, especially in those plots with plants also aggregated at the neighborhood-scale. We also hypothesized that both light and soil moisture would be more heterogeneous in the second year, due to plant maturity.

Methods

Study site

This experiment was conducted at a field site near Millville, Utah, USA (lat 41˚39'N, long 111˚48'W, 1370 m elevation). The soil at the site is a Ricks gravelly loam (coarse-loamy over sandy or sand-skeletal, mixed, superactive mesic Calcic Haploxerolls) (Bhattarai et al. 2008). Long-term mean annual precipitation (30 yr) averaged for three local weather stations was 480 mm (Leonard et al. 2008).

Study species

First introduced as a promising range grass to the Western U.S. in the 1930s, varieties of *A. cristatum* have been planted widely throughout the region (Hull and Klomp 1966; Pellant and Lysne 2005). *A. cristatum* exhibits a high level of both grazing (Sharp 1986) and drought tolerance (Caldwell and Richards 1986), and is strongly competitive with both other species (Aguirre and Johnson 1991; Pellant and Lysne 2005; Henderson and Naeth 2005) and itself (Salihi and Norton 1987; see chapter 4). In this experiment, we used the common 'Hycrest' cultivar (*A. cristatum* x *A. desertorum* [Fischer ex Link] Shultes, henceforth referred to as Hycrest crested wheatgrass), a hybrid crested wheatgrass that survives under greater competition and lower precipitation while

producing more biomass as compared to other crested wheatgrass cultivars (Asay et al. 1985).

Snake River wheatgrass (*Elymus wawawaiensis* J. Carlon & Barkworth) is found primarily in the Salmon, Snake, and Columbia River drainages of the Pacific Northwest, although *E. wawawaiensis* is commonly planted throughout the Intermountain region of the Western U.S. for forage in addition to restoration and reclamation projects (Jones 2008). Formally thought to be a variety of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), *E. wawawaiensis* was first recognized as a distinct taxon by Carlson (1986) based on cytological data. *E. wawawaiensis* is both drought and grazing tolerant, with an extensive root system and fair to good seedling vigor (Jones et al. 1991; Jones and Neilson 1997; Ogle et al. 2008). *E. wawawaiensis* is generally more productive, has higher seed production, and is easier to establish than many native Great Basin grasses (Carlson and Dewey 1987; Jones et al. 1991). In this experiment, we used the original 'Secar' cultivar of *E. wawawaiensis* (Ogle et al. 2008).

While we could find no published studies in which the competitive ability of *E. wawawaiensis* was directly evaluated relative to any cultivars of *A. cristatum*, *E. wawawaiensis* is almost certainly competitively inferior to *A. cristatum*. Numerous studies have found that *A. cristatum* is a superior competitor relative to other native Great Basin semi-arid bunchgrasses, including *P. spicata,* to which *E. wawawaiensis* is similar enough in form and function to be used as a surrogate in range plantings (Jones 2008; Mukherjee 2010). Seedlings of *E. wawawaiensis* are known to be less competitive than *A. cristatum* seedlings, and competition from weeds and aggressive introduced grass species (e.g. *A. cristatum*) may cause seedling mortality and stand failure (Ogle et al. 2008). *E.*

wawawaiensis may also be more susceptible to plant pathogens than *A. cristatum* (Griffin 1992). In a mixed community, there is a strong potential for interspecific competition between the two species since they essentially occupy the same niche (identical photosynthetic pathway [C3], similar stem and leaf architecture, canopy height, growing season). However, the actual dynamics of interspecific interactions between the two species are unknown, mirroring the broader gap in knowledge regarding the role of plant interactions in structuring arid and semi-arid plant communities (Phillips and MacMahon 1981; Fowler 1986; Armas and Pugnaire 2005; Brooker et al. 2008; Mokany et al. 2008).

Experimental design

Site preparation began in fall 2007, and included application of herbicide to control weeds and tilling to homogenize the soil. Seedlings of both species were germinated and grown to seedling stage in a greenhouse during the winter of 2008.

Ninety-six 2.5m x 2.5m experimental plots were established in spring 2008. We manipulated plant spatial patterns at both the community (plot) and neighborhood scales. Treatments consisted of a factorial combination of four types of community-scale patterns (Poisson random, regular grid, a fixed pattern of aggregation, and a variable pattern of aggregation) and three levels of neighborhood-scale aggregation (no aggregation, small aggregations, large aggregations) resulting in 12 treatments (Table 4), each with eight replicates, assigned in a completely randomized design to the 96 plots. In plots without community-scale aggregation, the inner 2 m x 2 m region of each 6.25 m^2 plot was sampled to reduce edge effects. In plots with community-scale aggregation, total plot-size was effectively scaled down to 2 m x 2 m due to centering of the aggregated

pattern within the plot, and the inner 1.5 m x 1.5 m region was sampled to reduce edge

effects (Table 1). Plants falling within the excluded plot edges were considered edge

plants (see below).

All spatial patterns were computer-generated using functions from the *splancs* and

spatstat packages for R (R Development Core Team 2007). Aggregations were generated

through simulated realizations of a Matérn cluster process using the *spatstat* package.

Each plot contained a total of 36 plants (18 of each grass species), and individual plants

of each species were randomly assigned to points with some constraints (e.g., a balanced

number of each species within each neighborhood-scale aggregation; see Table 1). The

effective density of grasses ($5.8 / m^2$ in plots without community-scale aggregation, and 9

$/ m^2$ in plots with community-scale aggregation) was determined by experimental

constraints and by scant published reports of Great Basin perennial grass densities in

intact communities (see chapter 4).

Seedlings were transferred to the field in May 2008, and planted using a wooden

frame that allowed for accurate replication ($\pm$ 2 cm) of computer-generated spatial

patterns. Plots were mapped to facilitate relocation and measurement of individual

grasses in both years of the experiment. Supplemental water was applied for one month

after planting. During that time, dead plants were counted as pre-experiment mortality

and replaced with extra greenhouse stock. Throughout the experiment, newly recruited

seedlings of the study species were removed, as were annual weeds and grasses.

<u>Data collection</u>

Aboveground biomass of each individual plant was non-destructively harvested at the peak of the growing season in late June of 2009 and 2010. Plants within plot edges were also harvested, although the biomass was discarded. Mortality was also recorded, but was extremely low (~1%) for the duration of the study and was not included in statistical analyses. For each plant, biomass was dried for approximately three weeks at 60˚C in drying ovens and subsequently weighed to the nearest hundredth of a gram. Total biomass for both species was calculated for each year, and mean biomass for each species was calculated for each plot in each year. Relative growth rate (RGR) was calculated for each plant from 2008 to 2009 and from 2009 to 2010 using an estimate of 0.1g for 2008 seedling weight and biomass values recorded for each individual plant in 2009 and 2010. Mean RGR was then computed for each species in each plot in each year.

PAR (μmol m^{-2}s^{-1}) was quantified using an AccuPAR model LP-80 PAR/LAI Ceptometer (Decagon). PAR was sampled at six locations in each plot, three on the west side of the plot and three on the south side of the plot, in the early afternoon on a cloudless day. At each sampling location, the probe was positioned approximately 2.5 cm above ground level. Each of the six measurements per plot represented the average of eighty sensors equally spaced along the 80 cm length of the probe. The coefficient of variation (a relative index of variability; Schlesinger et al. 1996) for PAR (CV_{PAR}) was calculated for each plot from the six measurements.

Soil moisture (%) in the upper 10-cm of the soil profile was quantified using an ML2x ThetaProbe Soil Moisture Sensor coupled to a HH2 Moisture Meter (Delta-T Devices). Percent soil moisture was sampled to a depth of 10 cm at nine locations within

a 3 x 3 grid that spanned the interior of each plot. The coefficient of variation for soil moisture (CV_{moist}) was calculated for each plot from the nine individual measurements. For both light and soil moisture sampling, measurements were taken at the same locations for both years on cloudless days prior to biomass sampling in late June 2009 and 2010.

Statistical analyses

Prior to analysis, three plots were removed from the dataset due to encroachment by invasive weeds and significant disturbance by small mammals. One additional mean CV_{moist} value was removed from the dataset since it was an unexplained outlier. The effects of *treatment*, *time*, and the *treatment* × *time* interaction on mean species biomass, species RGR, CV_{PAR} and CV_{moist} were analyzed using a split-plot in time approach. Data analyses were conducted using the GLIMMIX procedure in SAS/STAT software in the SAS system for Windows (version 9.2, SAS Institute 2008). Transformations (square-root) of the response variables were only required in the case of the abiotic response variables (CV_{PAR} and CV_{moist}) to stabilize the variance and to improve the normality of the residuals. Post-hoc contrasts and pair-wise mean comparisons were computed as needed to provide insight into patterns of significance; family-wise Type I error was controlled using the Tukey-Kramer method. All means are subsequently reported ± one S.E., with mean values and S.E.s of CV_{PAR} and CV_{moist} back-transformed to the original scale.

Results

<u>Above-ground biomass</u>

Independent of species, total harvested biomass across all plots increased by 68.1% from 67.76 kg in 2009 to 113.89 kg in 2010. Mean harvested biomass independent of species was greater in 2010 than in 2009 for all treatments, and the *treatment × year* interaction was significant (Table 6, P=0.0046). Treatment rankings varied minimally between years, although the increase in biomass differed among treatments. Pooled across years, there were strongly significant effects of *treatment* on mean biomass independent of species ($P<0.0001$, Table 6, Fig. 10a) with significant differences observed between certain treatments (Table 5). The highest mean biomass was observed in plots with regular spacing at the community-scale and no neighborhood-scale aggregation (treatment 4), while the lowest mean biomass was observed in plots aggregated at both community and neighborhood scales (treatment 12) (Table 5). The main effect of *year* on mean harvested biomass was also strongly significant ($P<0.0001$; Table 6); mean biomass increased by 69.4%, from 34.46 ± 0.76 g/plot in 2009 to 58.39 ± 1.58 g/plot (Fig. 10b).

Total harvested biomass of *E. wawawaiensis* decreased by 2.7% from 14.47 kg in 2009 to 14.08 kg in 2010. The *treatment × year* interaction was significant (P=0.0143, Table 6); mean harvested biomass was greater in 2010 than in 2009 for some treatments, while for other treatments the opposite was true. Because of the confounding nature of the interaction, we determined that it was invalid to interpret the main effects of *treatment* and *time* on mean harvested biomass of *E. wawawaiensis* (Fig. 11). However,

in both years mean harvested biomass appeared to be highest in plots with regular

spacing at the community-scale and no neighborhood-scale aggregation (treatment 4).

Total harvested biomass of Hycrest crested wheatgrass increased by 85.6% from

53.29 kg in 2009 to 98.90 kg in 2010. The *treatment × year* interaction was significant

(*P*=0.0484, Table 6): mean harvested biomass was greater in 2010 than in 2009 for all

treatments, and treatment rankings varied minimally between years. Pooled across years,

there were significant effects of *treatment* on mean biomass of Hycrest crested

wheatgrass (*P*<0.0001, Table 6, Fig. 10e) with significant pairwise differences observed

between certain treatments (Table 5). As in the analysis independent of species, the

highest mean biomass was again observed in plots with regular spacing at the

community-scale and no neighborhood-scale aggregation (treatment 4), and the lowest

mean biomass was observed in plots aggregated at both community and neighborhood

scales (treatment 12) (Table 5). The main effect of *year* on mean biomass of Hycrest

crested wheatgrass was significant (*P*<0.0001, Table 6); mean biomass increased by

83.9% from 54.66 ± 2.11 g/plot in 2009 to 100.53 ± 2.78 g/plot in 2010 (Table 5, Fig.

10f).

Relative growth rates

For relative growth rates of *E. wawawaiensis*, there was a significant *treatment ×*

year interaction (*P*=0.0255, Table 6); post-hoc tests (see Methods) revealed a significant

effect of *treatment* on mean RGR of *E. wawawaiensis* in 2009 (*P*=0.0206, Table 6, Fig.

12a) with significant differences observed between some treatments (Table 5), but no

evidence of treatment effects in 2010 (*P*=0.2895, Table 6). In 2009, the highest mean

RGR for *E. wawawaiensis* was observed in plots with regular spacing at the community-scale and no neighborhood-scale aggregation (treatment 4), while the lowest mean RGR was observed in plots with regularly spaced small aggregations (treatment 5), the same pattern as seen in mean biomass (Table 5). Pooled across treatments, there was a significant effect of *year* ($P<0.0001$, Table 6) as the mean relative growth rate of *E. wawawaiensis* declined from 4.39 ± 0.078 in 2009 to -0.041 ± 0.077 in 2010 (Fig. 12b).

Similar results were observed for Hycrest crested wheatgrass; there was a significant *treatment × year* interaction ($P<0.0001$, Table 6); post-hoc tests (see Methods) revealed a significant effect of treatment on mean RGR of Hycrest crested wheatgrass in 2009 ($P<0.0001$, Fig. 12c) with significant differences observed between some treatments (Table 5), but no evidence of treatment effects in 2010 ($P=0.2443$, Table 6). In 2009, the highest mean RGR for Hycrest crested wheatgrass was observed in plots with regular spacing at the community-scale and no neighborhood-scale aggregation (treatment 4), while the lowest mean RGR was observed in plots aggregated at both community and neighborhood scales (treatment 12), the same pattern as seen in biomass (Table 5). Pooled across treatments, there was a significant effect of *year* ($P<0.0001$, Table 6) as the mean RGR of Hycrest crested wheatgrass declined significantly from 6.00 ± 0.054 in 2009 to 0.56 ± 0.041 in 2010 (Fig. 12d).

Variability of light and soil moisture

For CV_{PAR}, the *treatment × year* interaction was significant ($P<0.0001$, Table 6). Based on post-hoc tests, we found that the effect of *treatment* on mean CV_{PAR} was significant in 2010 ($P<0.0001$) and that significant differences existed between only a

small subset of treatments (Table 5; Fig. 13a); no evidence of treatment effects was

detected for 2009 (P=0.1609, Table 6). The most variable light environments were

observed in plots with aggregated distribution of large aggregated neighborhoods

(treatments 9 and 12), while the least variable light environments were observed in plots

with regular distributions of large aggregated neighborhoods (treatment 6) (Table 5). The

main effect of *year* on mean CV_{PAR} was significant (P<0.0001, Table 6); mean back-

transformed CV_{PAR} increased by 45.0% from 0.40 ± 0.039 in 2009 to 0.58 ± 0.047 in

2010 (Fig. 13b).

For CV_{moist}, there was no evidence of a *treatment* × *year* interaction (P=0.1423,

Table 6). Pooled across years, there was a significant effect of *treatment* on CV_{moist}

(P=0.0024, Table 6, Fig. 13c). Similar to results for CV_{PAR}, significant differences were

observed between only a small subset of treatments (Table 5). The most variable soil

moisture environments were observed in plots with randomly distributed large aggregated

neighborhoods of grasses (treatment 3), while the least variable soil moisture

environments were observed in plots with regularly spaced small clusters of grasses

(treatment 5) and aggregated distribution of smaller aggregated neighborhoods (treatment

8) (Table 5). The main effect of *year* on mean CV_{moist} was significant (P=0.0014, Table

6); mean back-transformed CV_{moist} increased by 14.3% from 0.14 ± 0.0041 in 2009 to

0.16 ± 0.0044 in 2010 (Fig. 13d).

Discussion

Effect of treatment and time on aboveground
biomass and RGR

Past empirical studies of plant spatial patterns have generally focused on

investigating the effect of intraspecific aggregation on species coexistence (e.g. Stoll and

Prati 2001; Monzeglio and Stoll 2005; Mokany et al. 2008; Lamošová et al. 2010). Given

a plant community comprised of strong and weak competitors for limited resources, there

is convincing evidence that intraspecific aggregations reduce the frequency of

interspecific interactions thus reducing the effect of superior competitors on inferior

competitors and slowing competitive exclusion (Stoll and Prati 2001; Monzeglio and

Stoll 2005; Mokany et al. 2008).

However, although very few published studies exist that document spatial patterns

of semi-arid perennial bunchgrasses, intraspecific aggregations of perennial bunchgrasses

within Great Basin plant communities may be uncommon (Daubenmire 1970; Silvertown

et al. 1992; Adler et al. 2010) with some exceptions (e.g. purposely established

monocultures of *A. cristatum*, see chapter 4). A technical bulletin by Daubenmire (1970)

contained profile drawings of vascular plants along a transect in a Great Basin shrub-

steppe plant community; perennial grasses appear to have mostly heterospecific

neighbors. More recently, a study of long-term quadrat data from the Northern Great

Basin suggest that semi-arid communities dominated by shrubs and grasses are generally

well mixed at fine scales and characterized by interspecific, versus intraspecific

neighborhoods (Adler et al. 2010). Furthermore, both species used in this experiment are

components of diverse seed mixtures used for revegetation and range improvement that

have become increasingly popular as attempts are made by land managers to increase

plant diversity in Great Basin rangelands (e.g. Fansler and Mangold 2010). An

experimental framework that investigated the effects of intraspecific aggregation for

these two species could have addressed the effect of intraspecific aggregation on the

interactions between Hycrest crested wheatgrass and *E. wawawaiensis*, but the results

would have been less applicable to Great Basin plant communities. Instead, we utilized

realistic experimental communities with the two species planted in mixture in order to

test the effects of interspecific aggregation on community dynamics. While observational

studies of plant spatial patterns have been conducted in attempts to understand

community-structuring processes in the Western U.S. (e.g. Phillips and MacMahon 1981;

Weisberg et al. 2007; see also chapter 2 and chapter 4), we are aware of few other

empirical tests of the effect of plant spatial patterns on the dynamics of perennial Great

Basin plant communities (but see MacMahon 1997), and none with perennial grasses.

Given limited soil resources, both intra- and interspecific competition between

semi-arid perennial grasses may be intense (Booth et al. 2003; Leger 2008; see chapter

4). A past observational study of semi-arid range grasses hypothesized that regularity in

spatial patterns may arise as the direct result of this competition (Rayburn and Monaco

2011). The results of this study offer empirical support for this theory; pooled across

years, independent of species and for Hycrest crested wheatgrass, the highest mean

biomass values were observed in regularly-spaced plots lacking neighborhood-scale

aggregation (treatment 4), although these values were not always significantly different

from other treatments. Similar results were obtained for relative growth rates; pooled

across years, the highest RGRs for both species were observed in regularly-spaced plots

without neighborhood-scale aggregation (treatment 4), although again these values were not always statistically different from other treatments and the main effect of *treatment* on RGRs was only significant in the first year of the study. Competition was likely minimized in these plots relative to plots with more aggregated patterns, leading to significantly greater biomass production and, in the first year, significantly greater RGRs. In these plots, mean biomass was also influenced by neighborhood scale pattern: mean biomass of Hycrest crested wheatgrass in regularly-spaced plots without neighborhood-scale aggregation was consistently greater than mean biomass in regularly-spaced plots with aggregated neighborhoods. These results reveal that, in terms of biomass production in regularly-spaced plots, both community- and neighborhood-scale plant spatial patterns had effects on biomass production and growth rates.

Pooled across years, both species performed worse in plots with community-scale aggregation (treatments 6-12). Regardless of the neighborhood-scale pattern within these plots, there were no statistically significant differences in mean biomass independent of species or for Hycrest crested wheatgrass. These results suggest that community-level aggregation overwhelmed any effect of neighborhood-scale aggregation, likely because most plants in the community experienced aggregated, and therefore denser, local neighborhoods independent of our manipulation of neighborhood-scale patterns. Interspecific aggregation at the community-scale may have increased the frequency of both intra- and interspecific competition, although it is more likely that interspecific aggregations increased the magnitude of interspecific interactions, leading to suppression of both species and especially of the weaker competitor *E. wawawaiensis*.

Our results also strongly suggest that the effect of different spatial patterns was at least partially dependent on the competitive ability of the two perennial grasses. Hycrest crested wheatgrass generally performed better than *E. wawawaiensis* in all treatments and in both years, regardless of community-scale or neighborhood-scale spatial patterns. While interspecific aggregations lead to reductions in mean biomass and mean RGRs for the superior competitor Hycrest crested wheatgrass, reductions in mean RGRs were greater for the inferior competitor *E. wawawaiensis*. These results support recent studies of the effects of plant spatial patterns on grassland community dynamics that found that treatment effects were dependent on the competitive abilities of the species involved (Mokany et al 2008; Lamošová et al. 2010). For example, Mokany et al. (2008) studied the effects of spatial aggregation on resource use by native perennial grassland species; they found that while spatial aggregation affected the dynamics of light and soil moisture use by grasses, the effects were largely species-specific and depended on the relative strengths of interspecific versus intraspecific competition. Most recently, Lamošová et al. (2010) tested the effect of aggregation on the functioning of experimental assemblages of eight perennial grassland species by manipulating both species richness and spatial patterns. They found species in monoculture performed better in regular patterns due to a reduction in intraspecific competition, but that the performance of species in mixtures was dependent on the relative competitive strengths of the individual species.

Independent of species, there were strong effects of *year* on biomass; total biomass increased by 68.1% and mean biomass across all treatments increased by 69.4% from 2009-2010. However, the effects of *year* on total biomass, mean biomass and mean

RGRs were different for each species and were also apparently linked to the species'

competitive ability.

For the competitively superior species Hycrest crested wheatgrass, total biomass

increased by 85.6% from 2009-2010. Pooled across treatments, there was a significantly

positive effect of *year* on mean biomass, which increased by 83.9% from 2009-2010.

There was also a significantly negative effect of *year* on mean RGR for Hycrest crested

wheatgrass, which declined by 90.7% from 2009-2010 yet remained positive in 2010

(0.56 ± 0.041). In contrast, for the competitively inferior species *E. wawawaiensis*, total

biomass actually decreased by -2.70% from 2009-2010. In addition, there was a

significant effect of *time* on mean RGR, which declined by 100.9% from 2009-2010,

approximately equaling zero in 2010. These results provide additional evidence that

Hycrest crested wheatgrass is competitively superior to *E. wawawaiensis*, and suggest

that competitive exclusion of *E. wawawaiensis* would occur in aggregated plots given a

longer duration experiment.

Effect of treatment and time on variability of
light and soil moisture

Of all the potential factors influencing the distribution of light and soil moisture in

plant communities, the pattern of standing plant cover may be the most important

(Martens et al. 2000; Valladares 2003; Cantón et al. 2004). In this study, we observed the

specific changes in the variability of resource distribution wrought by random, regular,

and aggregated patterns at both community and neighborhood scales. Understanding the

effects of plant spatial patterns on the heterogeneity of light and soil moisture is

important, since resource heterogeneity can have significant effects on community and population dynamics (Harper 1997; Armas and Pugnaire 2005; Begon et al. 2006).

In this study, we found a highly significant effect of *treatment* on the variability of light near ground-level (mean CV_{PAR}). Our results suggest that a more heterogeneous distribution of semi-arid bunchgrasses may result in a more variable light environment near ground-level. There was also a significantly positive effect of *time* on mean CV_{PAR}, which increased significantly by 45.0% from 2009-2010. We attribute this effect to the increased size and density of grass canopies, especially Hycrest crested wheatgrass, in the second year. The *treatment x year* interaction was also significant for mean CV_{PAR}.

Although there was a significant effect of *treatment* on the variability of shallow soil moisture (mean CV_{moist}), the differences between treatments were less clear. While the distribution of light is primarily a function of the characteristics of above-ground biomass (e.g. plant spatial patterns, plant height, canopy diameter, leaf architecture), the distribution of shallow soil moisture may depend on various factors including soil characteristics (e.g. particle size and water-holding capacity), species-specific plant anatomy and physiology (e.g. root type and distribution, transpiration rates, stomata size), other abiotic factors such as wind, and indirect effects of above-ground biomass (e.g. reduced evaporation through shade, sunflecks, leaf architecture). There was also a significantly positive effect of time on mean CV_{moist}, which increased significantly by 14.3% from 2009-2010. As with CV_{PAR}, we attribute this effect to increased above-ground biomass of grasses (especially Hycrest crested wheatgrass in the second year) that likely produced concomitant increases in root biomass and increased variability in soil moisture distribution.

Generally, more heterogeneous patterns of plant canopy cover lead to more canopy and/or root gaps, which may be especially important for colonization by both native and invasive species (Bullock 2000; Blair et al. 2010). Competition for light and soil moisture may be reduced in gaps between perennial plants in Great Basin plant communities, potentially facilitating recruitment of poorly competitive native species but also invasion of troublesome annual grasses such as *Bromus tectorum* L. (cheatgrass). In recognition of this possible relationship, we initiated a second experiment in 2010 that takes advantage of the spatial treatments used for this study to test for the effect of community- and neighborhood-scale spatial patterns on the germination, growth, survival, and reproduction of *B. tectorum*.

Conclusion

Our results demonstrate the effects of community- and neighborhood-scale plant spatial patterns on community dynamics within experimental semi-arid perennial bunchgrass communities. Both the strong competitor Hycrest crested wheatgrass and the weaker competitior *E. wawawaiensis* performed better in regularly-spaced plots that lacked neighborhood-scale aggregation as compared to plots with random or aggregated patterns at either scale. In addition, we show that effects may be species-specific and strongly linked to a given species' competitive ability. In general, *E. wawawaiensis* performed more poorly than Hycrest crested wheatgrass in all treatments, especially in aggregated treatments where the effects of interspecific competition were presumably greater.

Spatial treatments also strongly influenced the distribution of light and soil moisture, with more heterogeneous patterns of plants resulting in a more variable light environment. The heterogeneity of both abiotic resources also increased in the second year of the study, which we attribute to the effect of increased above- and below-ground biomass.

The results of this study support past research on the effects of plant spatial patterns, but are unique in that we used realistic experimental communities comprised of interspecific mixtures of co-occurring perennial grasses. Our findings may lead to a better understanding on the effects of plant patterns in water-limited grasslands, with additional relevance in the Great Basin region of the Western U.S. where both species commonly occur.

References

Aguirre L, Johnson DA (1991) Influence of temperature and cheatgrass
    competition on seedling development of two bunchgrasses. J Range Manage
    44:347-354

Adler PB, Ellner SP, Levine JM (2010) Coexistence of perennial plants: an
    embarrassment of niches. Ecol Lett 13:1019-1029

Armas KH, Pugnaire FI (2005) Plant interactions govern population dynamics in
    a semi-arid plant community. J Ecol 93:978-989

Asay KH, Dewey DR, Gomm FB, Johnson DA, Carlson JR (1985)
    Registration of 'Hycrest' crested wheatgrass. Crop Sci 25:368-369

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to

ecosystems. Blackwell Publishing Ltd, Oxford, UK

Bhark EW, Small EE (2003) Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems 6:185-196

Bhattarai K, Johnson DA, Jones TA, Conners KJ, Gardner DR (2008) Physiological and morphological characterization of basalt milkvetch (*Astragalus filipes*): basis for plant improvement. Rangeland Ecol. Manage. 61:444-455

Blair BC, Letourneau DK, Bothwell SG, Hayes GF (2010) Disturbance, resources, and exotic plant invasion: gap size effects in a redwood forest. Madroño 57:11-19

Bolker BM, Pacala SW, Neuhauser C (2003) Spatial dynamics in model plant communities: What do we really know? Am. Nat. 162:135-148

Booth MS, Caldwell MM, Stark JM (2003) Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. J. Ecol. 91:36-48

Breshears DD, Rich PM, Barnes FJ, Campbell K (1997) Overstory imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol. App. 7:1201–1215

Breshears DD, Nyhan JW, Heil CE, Wilcox BP (1998) Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. Int. J. Plant Sci. 153:425–433

Brooker RW et al. (2008) Facilitation in plant communities: the past, the present, and the future. J. Ecol. 96:18-34

Bullock JM (2000) Gaps and seedling colonization. In: Fenner M (ed) Seeds - The

    Ecology of regeneration in plant communities. CAB International, Wallingford,

    UK, pp 375-395

Caldwell MM, Richards H (1986) Ecophsiology of crested wheatgrass: a

    comparative study with bluebunch wheatgrass. In: Johnson KL (ed) Crested

    wheatgrass: its values, problems, and myths. Symposium proceedings. Utah State

    University, Logan, UT, USA, pp 165-167

Cantón Y, Solé-Benet A, Domingo F (2004) Temporal and spatial patterns of soil

    moisture in semiarid badlands of SE Spain. J. Hydrol. 285:199-214

Carlson JR (1986) A study of morphological variation within *Pseudoroegneria spicata*

    (Pursh) A. Löve (Poaceae: Triticeae). MS thesis, Oregon State University,

    Corvallis, OR

Carlson JR, Dewey DR (1987) Characterization of *Elymus lanceolatus* ssp.

    wawawai and its potential as a range forage grass. In: American Society

    of Agronomy Abstracts. Madison, WI, p 59

Czárán T, Bartha S (1992) Spatiotemporal dynamic models of plant populations and

    communities. Trends Ecol. Evol. 7:38-42

Daubenmire R (1970) Steppe vegetation of Washington. Washington Agricultural

    Experiment Station Technical Bulletin 62, Pullman, WA

De Boeck, H J, Nijs I, Lemmens CMHM, Ceulemans R (2006) Underlying

    effects of spatial aggregation (clumping) in relationships between plant diversity

    and resource uptake. Oikos 113:269-278

Dunstan PK, Johnson CR (2003) Competition coefficients in a marine epibenthic

assemblage depend on spatial structure. Oikos 100:79–88

Fajardo A, McIntire EJB (2007) Distinguishing microsite and competition processes in tree growth dynamics: an a priori spatial modeling approach. Am. Nat.165:647-661

Fansler VA, Mangold JM (2010) Restoring native plants to crested wheatgrass stands. Restor. Ecol. 19:16–23

Fowler NJ (1986) The role of competition in plant communities in arid and semi-arid regions. Annu. Rev. Ecol. Syst. 17:89-110

Griffin GD (1992) Pathological effects of *Pratylenchus neglectus* on Wheatgrasses. J. Nematol. 24:442–449

Haase P, Pugnaire FI, Clark SC, Incoll LD (1996) Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. J. Veg. Sci. 7:527-534

Harper JL (1997) Population biology of plants. Academic Press, London

Hegazy AK, Elfiky A, Kabiel HF (2005) Spatial pattern and mulching effect of *Anastatica hierochuntica* L. on structure and function of some desert plants. In: Harper JDI, An M, Wu H, Kent JH (eds) Proceedings of the 4th World Congress on Allelopathy. Charles Sturt University, NSW, Australia, pp 21-26

Henderson DC, Naeth MA (2005) Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biol. Invasions 7:639-650

Hull AC Jr, Klomp GJ (1966) Longevity of crested wheatgrass in the sagebrush-grass type in southern Idaho. J. Range Manage 19:5-11

Kenkel NC (1988) Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. Ecol. 69:1017-1024

Klausmeier CA (1999) Regular and irregular patterns in semiarid vegetation. Science 284:1826-1828

Jones TA (2008) Notice of release of 'Discovery' Snake River wheatgrass. Native Plants J. 9:99-101

Jones TA, Nielson DC, Carson JR (1991) Developing a grazing-tolerant native grass for bluebunch wheatgrass sites. Rangelands 13:147-150

Jones TA, Nielson DC (1997) Defoliation tolerance of bluebunch and Snake River Wheatgrasses. Agron. J. 89:270-275

Lamošová T, Doležal J, Lanta V, Leps J (2010) Spatial pattern affects diversity-productivity relationships in experimental meadow communities. Acta Oecol. 36:325-332

Leger EA (2008) The adaptive value of remnant native plants in invaded communities: an example from the Great Basin. Ecol. Appl. 18:1226-1235

Leonard ED, Monaco TA, Stark JM, Ryel RJ (2008) Invasive forb, annual grass, and exotic shrub competition with three sagebrush-steppe growth forms: acquisition of a spring ^{15}N tracer. Invasive Plant Sci. Manage. 1:168–177

Lortie CJ, Ellis E, Novoplansky A, Turkington R (2005) Implications of spatial pattern and local density on community-level interactions. Oikos 109:495-502

MacMahon JA (1997) Ecological restoration. In: Meffe GK, Carroll CR (eds) Principles of conservation biology, 2nd edn. Sinauer Associates, Inc., Sunderland, MA, pp 479-511

Maestre FT, Escudero A, Martinez I, Guerreros C, Rubio A (2005) Does spatial

pattern matter to ecosystem functioning? Insights from biological soil crusts. Funct. Ecol. 19:566-573

Martens SN, Breshears DD, Meyer CW, Barnes FJ (1997) Scales of above- and below-ground competition in a semiarid woodland as detected from spatial pattern. J. Veg. Sci. 8:655–664

Martens SN, Breshears DD, Meyer CW (2000) Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecol. Model. 126:79-93

Monzeglio U, Stoll P (2005) Spatial patterns and species performance in experimental plant communities. Oecologia 145:619-628

Mokany, K, Ash J, Roxburgh S (2008) Effects of spatial aggregation on competition, complementarity, and resource use. Austral Ecol. 33:261-270

Mukherjee JR (2010) Evaluating native wheatgrasses for restoration of sagebrush steppes. PhD dissertation, Utah State University, Logan, UT

Murrell DJ, Purves DW, Law R (2001) Uniting pattern and process in plant ecology. Trends Ecol. Evol. 16:529-530

Murrell DJ, Law R (2003) Heteromyopia and the spatial coexistence of similar competitors. Ecol. Lett. 6:48-59

Ogle DG, Stannard M, Jones TA (2008) Snake River Wheatgrass. USDA NRCS, Boise, ID

Pacala SW, Tilman D (1994) Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. Am. Nat. 143: 222-257

Pacala SW, Deutschman DH (1995) Details that matter: the spatial distribution of

individual trees maintains forest ecosystem function. Oikos 74:357-365

Pacala SW (1997) Dynamics of plant communities. In: Crawley MJ (ed) Plant ecology. Blackwell Scientific, Oxford, UK, pp 532-555

Pellant M, Lysne CR (2005) Strategies to enhance plant structure and diversity in crested wheatgrass seedings. US Department of Agriculture, Forest Service Proceedings RMRS-P-38, pp 16-33

Perry GLW, Enright NJ, Miller BP, Lamont BB (2008) Spatial patterns in species-rich sclerophyll shrublands of southwestern Australia. J. Veg. Sci. 19:705-716

Perry GLW, Enright NJ, Miller BP, Lamont BB (2009) Nearest-neighbor interactions in species-rich shrublands: the roles of abundance, spatial patterns and resources. Oikos 118:161-174

Phillips DL, MacMahon JA (1981) Competition and spacing patterns in desert shrubs. J. Ecol. 69:97-115

Rodriguez-Iturbe I, D'Odorico P, Porporato A, Ridolfi L (1999) On the spatial and temporal links between vegetation, climate and soil moisture. Water Resour. Res. 12:3709-3722

Sala OE, Aguiar MR (1996) Origin, maintenance, and ecosystem effect of vegetation patches in arid lands in rangelands in a sustainable biosphere. In: N. West N (ed) Proceedings of the Fifth International Rangeland Congress Vol. 2. Society for Range Management, Denver, CO, pp 29-32

Salihi DO, Norton BE (1987) Survival of perennial grass seedlings under intensive grazing in semi-arid rangelands. J. App. Ecol. 24:145-151

Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial

   pattern of soil nutrients in desert ecosystems. Ecol. 77:364-374

Schurr FM, Bossdorf O, Milton SJ, Schumacher J (2004) Spatial pattern formation in

   semi-arid shrubland: a priori predicted versus observed pattern characteristics.

   Plant Ecol. 173:271-282

Seifan M, Kadmon R (2006) Indirect effects of cattle grazing on shrub spatial

   pattern in a Mediterranean scrub community. Basic App. Ecol. 7:496-506

Sharp LA (1986) Crested wheatgrass: its values, problems and myths. In: Johnson KL

   (ed) Crested wheatgrass: its values, problems, and myths. Symposium

   proceedings. Utah State University, Logan, UT, USA, pp 3-6

Silvertown J, Holtier S, Johnson J, Dale P (1992) Cellular automaton models of

   interspecific competition for space – the effect of pattern on process. J. Ecol.

   80:527-534

Skarpe C (1991) Spatial patterns and dynamics of woody vegetation in an arid savanna.

   J. Veg. Sci. 2:565-572

Stoll P, Prati D (2001) Intraspecific aggregation alters competitive interactions in

   experimental plant communities. Ecol. 82:319-327

Stoll P, Bergius E (2005) Pattern and process: competition causes regular spacing

   of individuals within plant populations. J. Ecol. 93:395-403

Tilman D, Kareiva P (1997) The role of space in population dynamics and

   interspecific interactions. Princeton University Press, Princeton, NJ

Tirado R, Pugnaire FI (2003) Shrub spatial aggregation and consequences for

   reproductive success. Oecologia 136:296-301

Turnbull LA, Coomes DA, Purves DW, Rees M (2007) How spatial structure

    alters population and community dynamics in a natural plant community. J. Ecol.

    95:79-89

Valiente-Banuet A, Verdú M (2008) Temporal shifts from facilitation to competition

    occur between closely related taxa. J. Ecol. 96:489-494

Valladares F (2003) Light heterogeneity and plants: from ecophysiology to species

    coexistence and biodiversity. Prog. Bot. 64:439-471

Went FW (1942) The dependence of certain annual plants on shrubs in Southern

    California deserts. B. Torrey Bot. Club 69:100-114

Weisberg PJ, Lingua E, Pillai RB (2007) Spatial patterns of pinyon-juniper

    woodland expansion in Central Nevada. Range. Ecol. Manage 60:115-124

West NE (1983) Temperate deserts and semi-deserts. Elsevier, Amsterdam

West NE, Hea KH, Harniss RO (1979) Plant demographic studies in sagebrush-

    grass communities of southeastern Idaho. Ecol. 60:376-388

West NE (1988) Intermountain deserts, shrub steppes, and woodlands. In: Barbour MG,

    Billings WD (eds) North American terrestrial vegetation. Cambridge University

    Press, Cambridge, pp 209-230

Wiegand T, Gunatilleke CVS, Gunatilleke IAUN, Okuda T (2007) Analyzing the spatial

    structure of a Sri Lankan tree species with multiple scales of clustering. Ecol.

    88:3088–3102

Table 4. Description of the twelve experimental treatments. For each treatment, notation (X/Y) represents the number of plants from each species (*E. wawawaiensis* and Hycrest crested wheatgrass) planted within the entire plot (in plots with neighborhood-level randomness) or within each cluster (in plots with neighborhood-level aggregation). In cases where neighborhood-scale patterns were aggregated, clusters of grasses were randomly distributed, spaced evenly apart, or clustered together according to the community-scale pattern.

Plot-level pattern	Neighborhood-level aggregation		
	None	**Small aggregations**	**Large aggregations**
Random	Random pattern of 36 plants (18/18) (code = 1)	Random pattern of nine clusters of four plants (2/2) (code = 2)	Four clusters of nine plants (5/4, 4/5, 5/4, 4/5) randomly placed in plot (code = 3)
Regular	36 plants (18/18) planted in a 6 x 6 grid (code = 4)	Nine clusters of four plants (2/2) placed in equally spaced 3 x 3 grid (code = 5)	Four clusters of nine plants (5/4, 4/5, 5/4, 4/5) placed in equally spaced 2 x 2 grid (code = 6)
Aggregated (fixed; a single pattern replicated eight times)	Aggregated pattern of 36 plants (18/18) (code = 7)	Aggregated pattern of nine clusters of four plants (2/2) (code = 8)	Aggregated pattern of four clusters of nine plants (5/4, 4/5, 5/4, 4/5) (code = 9)
Aggregated (eight different aggregated patterns)	Aggregated pattern of 36 plants (18/18) (code = 10)	Aggregated pattern of nine clusters of four plants (2/2) (code = 11)	Aggregated pattern of four clusters of nine plants (5/4, 4/5, 5/4, 4/5) (code = 12)

Table 5. Comparisons of means between individual treatments for biomass, relative growth rates, CV_{PAR}, and CV_{moist}. Means with unique letters within a column represent significant statistically significant differences. Letters are not shown for mean biomass of *E. wawawaiensis* because of the confounding *treatment × time* interaction (see Results, Fig. 2). See Table 1 for explanation of treatments. Means are reported ± one S.E. (back-transformed in the case of CV_{PAR} and CV_{moist}).

Trt	Both spp.	Hycrest crested wheatgrass		*Elymus wawawaiensis*		Abiotic variables	
	Biomass (g)	Biomass (g)	2009 RGR	Biomass (g)	2009 RGR	CV_{PAR}	CV_{moist}
1	58.81 ± 3.44^{abc}	86.98 ± 5.65^{abc}	6.17 ± 0.15^{abc}	19.52 ± 2.14	4.55 ± 0.25^{ab}	0.44 ± 0.00018^{ab}	0.16 ± 0.00066^{ab}
2	62.29 ± 3.44^{ab}	104.41 ± 5.65^{ab}	6.36 ± 0.15^{ab}	16.95 ± 2.14	4.62 ± 0.25^{ab}	0.42 ± 0.00018^{ab}	0.16 ± 0.00066^{ab}
3	48.86 ± 3.44^{bcd}	77.85 ± 5.65^{cd}	5.91 ± 0.15^{abc}	17.94 ± 2.14	4.38 ± 0.25^{ab}	0.49 ± 0.00018^{ab}	0.17 ± 0.00066^{a}
4	68.19 ± 3.67^{a}	109.70 ± 6.04^{a}	6.61 ± 0.16^{a}	26.64 ± 2.28	5.29 ± 0.27^{a}	0.41 ± 0.00021^{ab}	0.13 ± 0.00066^{ab}
5	36.47 ± 3.44^{d}	64.66 ± 5.65^{cd}	5.61 ± 0.15^{c}	8.48 ± 2.14	3.81 ± 0.25^{b}	0.47 ± 0.00018^{ab}	0.12 ± 0.00066^{b}
6	44.22 ± 3.44^{cd}	80.27 ± 5.65^{bcd}	6.14 ± 0.15^{abc}	14.66 ± 2.14	4.29 ± 0.25^{ab}	0.41 ± 0.00018^{b}	0.15 ± 0.00066^{ab}
7	42.15 ± 3.44^{d}	78.86 ± 5.65^{cd}	6.19 ± 0.15^{abc}	17.21 ± 2.14	4.76 ± 0.25^{ab}	0.46 ± 0.00018^{ab}	0.16 ± 0.00066^{ab}
8	41.20 ± 3.44^{d}	71.10 ± 5.65^{cd}	5.89 ± 0.15^{bc}	9.84 ± 2.14	4.04 ± 0.25^{b}	0.55 ± 0.00018^{ab}	0.12 ± 0.00066^{b}
9	41.01 ± 3.97^{d}	64.93 ± 6.52^{cd}	5.72 ± 0.17^{bc}	13.03 ± 2.47	4.06 ± 0.29^{b}	0.58 ± 0.00027^{a}	0.15 ± 0.00066^{ab}

10	41.95 ± 3.44^d	64.22 ± 5.65^{cd}	5.96 ± 0.15^{abc}	13.85 ± 2.14	4.53 ± 0.25^{ab}	0.52 ± 0.00018^{ab}	0.13 ± 0.00066^{ab}
11	44.59 ± 3.44^{cd}	72.44 ± 5.65^{cd}	5.90 ± 0.15^{abc}	10.88 ± 2.14	4.14 ± 0.25^b	0.54 ± 0.00018^{ab}	0.13 ± 0.00066^{ab}
12	35.50 ± 3.44^d	56.59 ± 5.65^d	5.55 ± 0.15^c	13.52 ± 2.14	4.30 ± 0.25^{ab}	0.58 ± 0.00018^a	0.16 ± 0.00066^{ab}

Table 6. Summary of statistical results from analysis of effect of treatment and year on biomass (independent of species and for species individually) and relative growth rate (for each study species), as well as CV_{PAR} and CV_{moist}.

| Test	df_{num}	df_{den}	F value	Pr > F
Biomass				
Treatment	11	81	8.74	<0.0001
Year	1	81	391.91	<0.0001
Treatment x year	11	81	2.74	0.0046
E.wawawawiensis biomass				
Treatment	11	81	4.96	<0.0001
Year	1	81	0.16	0.6874
Treatment x year	11	81	2.35	0.0143
Hycrest crested wheatgrass biomass				
Treatment	11	81	7.68	<0.0001
Year	1	81	509.26	<0.0001
Treatment x year	11	81	1.92	0.0484
E.wawawawiensis RGR				
Treatment	11	81	1.29	0.02437
Treatment (2009)	11	81	2.22	0.0206
Treatment (2010)	11	81	1.22	0.2895
Year	1	81	1776.77	<0.0001
Treatment x year	11	81	2.15	0.0255
Hycrest crested wheatgrass RGR				
Treatment	11	81	1.29	0.2478
Treatment (2009)	11	81	4.12	<0.0001
Treatment (2010)	11	81	1.29	0.2443
Year	1	81	7828.57	<0.0001
Treatment x year	11	81	4.13	<0.0001
CV_{PAR}				
Treatment	11	81	2.85	0.0033
Treatment (2009)	11	81	1.47	0.1609
Treatment (2010)	11	81	4.54	<0.0001
Year	1	81	199.74	<0.0001
Treatment x year	11	81	3.44	0.0006
CV_{moist}				
Treatment	11	81	2.96	0.0024
Year	1	80	10.89	0.0014
Treatment x year	11	80	1.52	0.1423
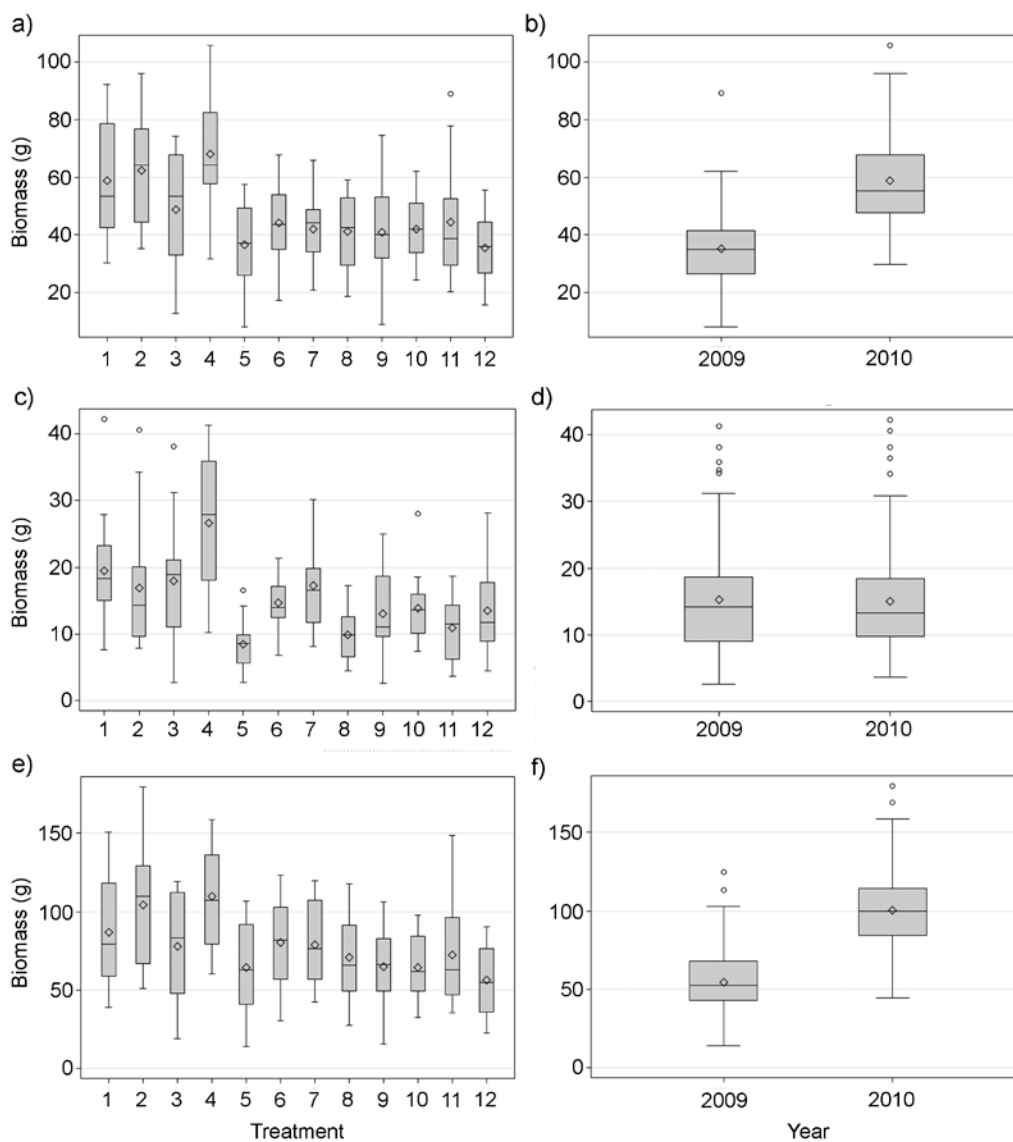
Fig. 10. Boxplots of a) above-ground biomass (AGB) (g) for both species combined by treatment, pooled across study years ($P<0.0001$), b) AGB for both species in each year, pooled across treatments ($P<0.0001$), c) AGB for *E. wawawaiensis* by treatment, pooled across years ($P<0.0001$), d) AGB for *E. wawawaiensis* in each year, pooled across treatments ($P=0.6874$), e) AGB for Hycrest crested wheatgrass by treatment, pooled across years ($P<0.0001$), and f) AGB for Hycrest crested wheatgrass in each year, pooled

across treatments (P<0.0001). Note that the confounding *treatment × time* interaction for mean biomass of *E. wawawaiensis* (see Results, Fig. 2) precluded interpretation of main effects of *treatment* and *time*.
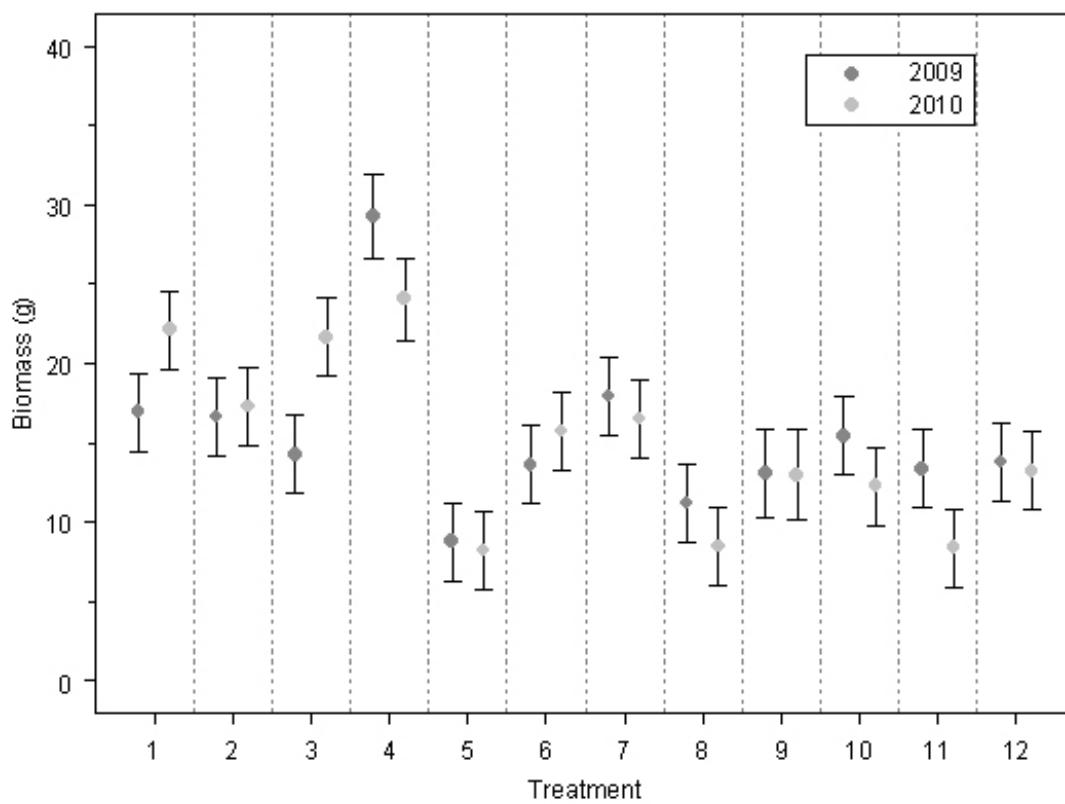
Fig. 11. Visual evidence of the the confounding *treatment × time* interaction for mean

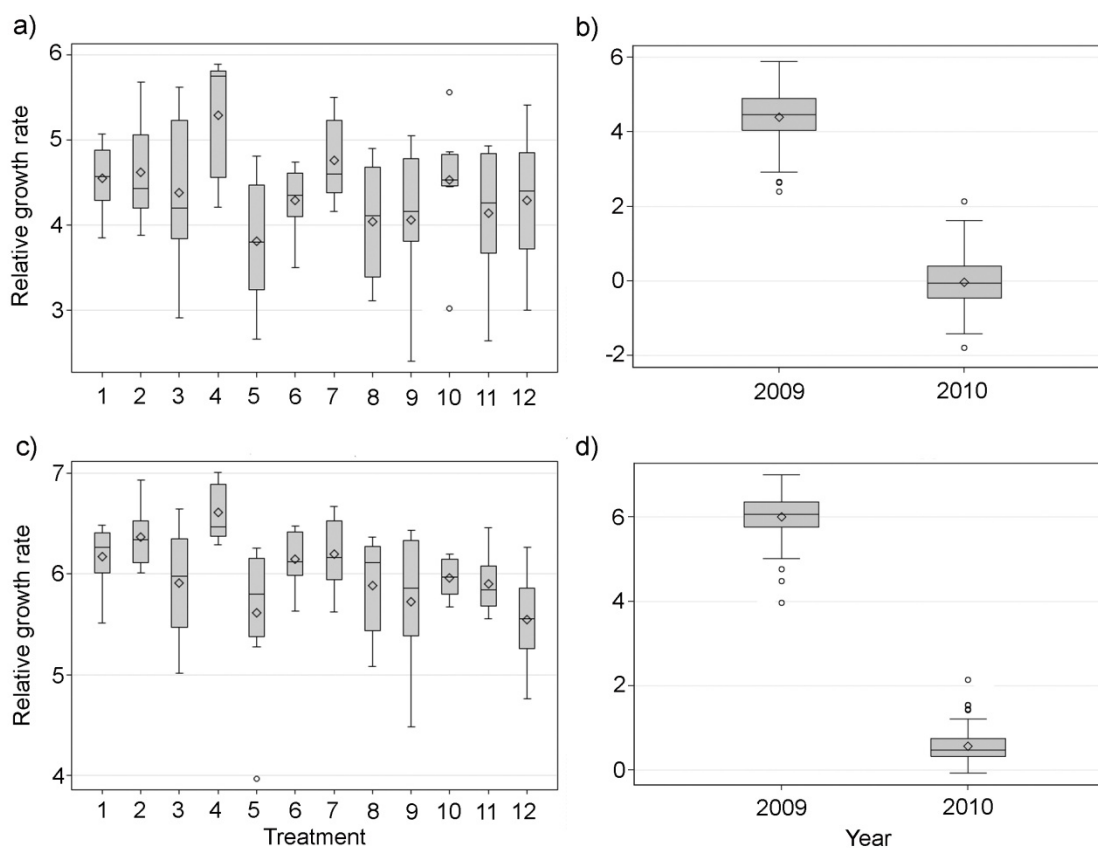biomass (g) of *E. wawawaiensis* (see Results).

Fig. 12. Boxplots of a) *E. wawawaiensis* relative growth rate (RGR) by treatment in 2009 (*P*<0.0001), b) *E. wawawaiensis* RGR in each study year, pooled across treatments (*P*<0.0001), c) Hycrest crested wheatgrass RGR by treatment in 2009 (*P*<0.0001), and d) Hycrest crested wheatgrass RGR in each study year, pooled across treatments (*P*<0.0001).
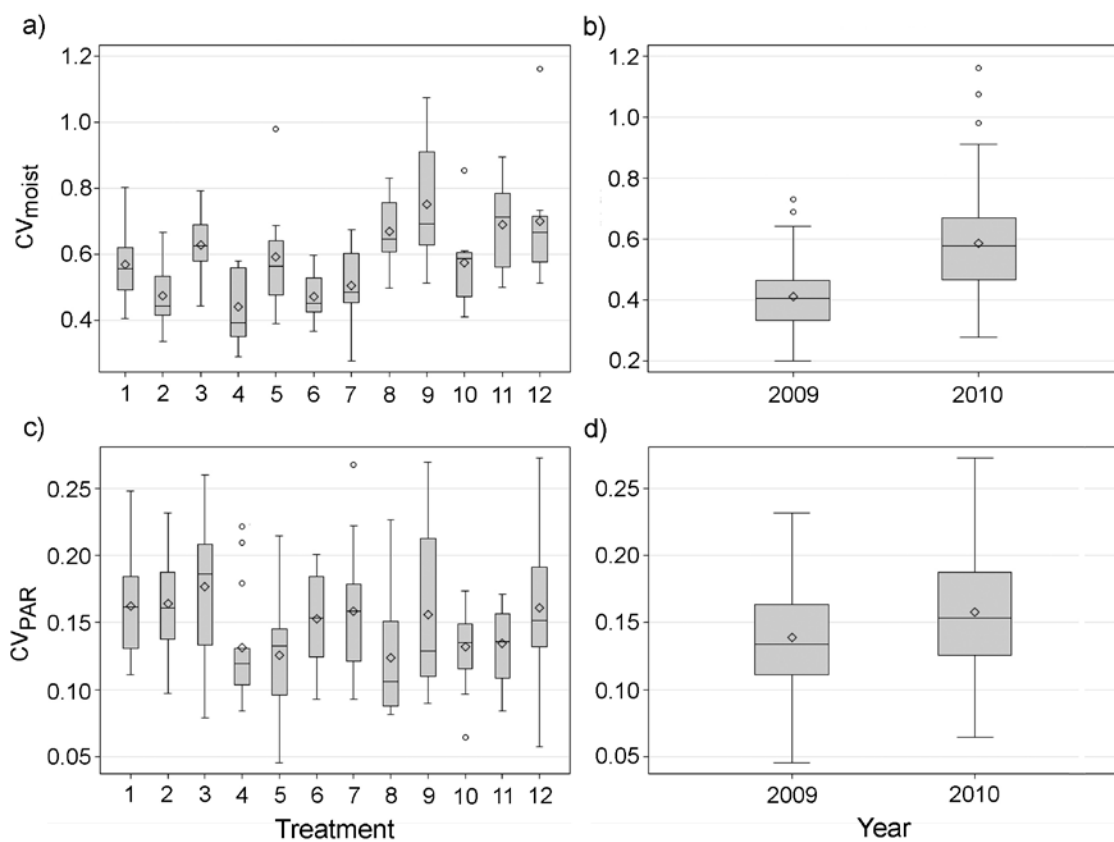
Fig. 13. Boxplots of a) CV_{PAR} by treatment in 2010 ($P<0.0001$); b) CV_{PAR} in each of the study years, pooled across treatments ($P<0.0001$); c) CV_{moist} by treatment, pooled across both study years ($P=0.0024$); d) CV_{moist} in each of the study years, pooled across treatments ($P=0.0014$)

CHAPTER VI

CONCLUSIONS

One of the central goals of plant ecology remains to elucidate the processes by which plant communities are structured in space and time. Theoretical, observational, and empirical studies have in part revealed the complex interplay of plant patterns and ecological processes that shape communities. However, both the causes and consequences of plant spatial patterns remain important topics of research in plant ecology. While there is a rich history of studies that have examined the means by which plant spatial patterns are formed through various ecological processes, methodological advances in data collection and analysis presented here and in other recent studies discussed throughout this dissertation set the stage for more advanced research on pattern formation, especially in more arid communities in which plants tend to occur as discrete individuals. Future research on pattern formation will almost certainly focus on the effects of anthropogenic activities (e.g., disturbance, development, climate change) on the formation and maintenance of plant spatial patterns. Conversely, the analysis of dynamic plant patterns may bring new insight into the type and magnitude of processes that are important in structuring plant communities.

Future research on the causes and consequences of plant spatial patterns in semi-arid plant communities will likely benefit from the acquisition of precise spatial data on plant species, size, and location (x, y coordinates and elevation) as described in this dissertation and elsewhere. In addition, such data will aid spatially-explicit population

studies, since mortality, growth, seed production and recruitment may be tracked for many individual plants within a community over long temporal scales.

Besides advancing basic ecological research on connections between plant patterns and ecological processes, the research detailed in this dissertation has various potential applications related to the management and conservation of semi-arid plant communities. The data collection procedure I present in the first data chapter, involving the use of field-portable GPS systems to efficiently and precisely obtain spatial data on plant species, size, and location, could be utilized by scientists and land managers to rapidly map plant communities in support of long-term monitoring objectives, such as tracking the status of invasive or rare species and/or plant community dynamics in response to disturbance or changes in temperature and precipitation regimes associated with current and future climate change. Once precise spatial data has been obtained, analyses of spatial patterns of species diversity (data chapter 2) could be conducted to determine if any species within a given community has a disproportionate effect on local diversity. Species that have such an effect may be important targets of conservation or restoration efforts, especially those that seek to maintain or improve plant diversity within a community. Precise spatial data may also be used to test hypotheses regarding the spatiotemporal scale at which various processes act to structure plant communities (data chapter 3), informing both basic and applied ecological research of dynamic managed communities. Finally, the results of the novel field experiment described in the fourth data chapter provide new insight on effects of plant spatial patterns in mixed communities on both plant performance and the distribution of abiotic resources. My results support past research on the effects of plant spatial patterns, but are unique in that

the experiment involved well-replicated, realistic experimental communities comprised of interspecific mixtures of co-occurring perennial grasses. Our findings may lead to a better understanding on species-specific effects of plant patterns in water-limited grasslands, such as those in the Great Basin region of the Western U.S.

In conclusion, each of the studies that make up this dissertation were conducted to address gaps in experimental design, data collection, and/or data analysis. I hope that this work has advanced the study of plant spatial patterns in some small way, and that the techniques I have described will be adopted and adapted by future researchers.

APPENDIX

September 7, 2011

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Dear Dr. Katja Schiffers;

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I graduated in May 2011, and am in the process of turning in my revised dissertation.

I am requesting your permission as a co-author to include our recently published paper in the journal Plant Ecology as a chapter in my dissertation.

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Rayburn AP, Schiffers K, and Schupp EW (2011) Use of precise spatial data for describing spatial patterns and plant interactions in a diverse Great Basin shrub community. Plant Ecol. DOI: 10.1007/s11258-010-9848-0.

Signed_____Katja Schiffers____

Date____12 September 2011_____

Fee_____Free_____

March 18, 2011

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To *Plant Ecology* Permissions Editor:

I am preparing my dissertation in the Department of Wildland Resources at Utah State University. My intent is to complete my Ph.D. degree in spring 2011.

An article, *Use of precise spatial data for describing spatial patterns and plant interactions in a diverse Great Basin shrub community*, of which I am first author , and which appeared in your journal (2011; DOI: 10.1007/s11258-010-9848-0), reports an essential part of my dissertation research. I would like permission to reprint it as a chapter in my dissertation. Reprinting the chapter may require some minor revisions related to formatting for the dissertation. Please note that USU sends dissertations to Bell & Howell Dissertation Services to be made available for reproduction.

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To *Rangeland Ecology and Management* Permissions Editor:

I am preparing my dissertation in the Department of Wildland Resources at Utah State University. My intent is to complete my Ph.D. degree in spring 2011.

An article, *Linking plant spatial patterns and ecological processes in grazed Great Basin plant communities*, of which I am first author , and which is in press for a forthcoming issue of your journal (2011; DOI: 10.1007/s11258-010-9848-0), reports an essential part of my dissertation research. I would like permission to reprint it as a chapter in my dissertation. Reprinting the chapter may require some minor revisions related to formatting for the dissertation. Please note that USU sends dissertations to Bell & Howell Dissertation Services to be made available for reproduction.

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Rayburn, A. P., and T. A. Monaco. In press. Linking plant spatial patterns and ecological processes in grazed Great Basin plant communities. *Rangeland Ecology and Management* DOI: 10.2111/REM-D-10-00130.1.

Signed__Valerie Pierce / Publishing Coordinator_

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CURRICULUM VITAE

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Logan, UT 84322-5200

Education.

- Ph.D. (in progress); Ecology, Utah State University (advisor: Eugene W. Schupp); anticipated graduation in Spring 2011.

- M.S.; Ecology and Evol. Biology, Iowa State University (advisor: Lisa A. Schulte), 2006

- B.A. (*cum laude*); Biology, Austin College (Sherman, TX), 2001

Professional Experience.

- Ph.D. Graduate Research Assistant, Utah State University, 2006-present.

- M.S. Graduate Research Assistant, Iowa State University, 2004-2006

- Field Technician, Jornada Long Term Ecological Research (LTER) Site, 2001

- Field Technician, Smithsonian Tropical Research Institute, Panama, 1999

- Field Supervisor, Cedar Creek LTER, 1999

- NSF Research Experience for Undergraduates (REU) Program, Cedar Creek LTER, 1999

- Field Technician, Cedar Creek LTER, 1998

Research Interests. Connecting ecological patterns and processes across spatiotemporal scales; spatial statistics; community and population dynamics; restoration ecology; disturbance; conservation of biodiversity; vegetation response to climate change; landscape ecology

Grants.

Sigma Xi Research Grant

- 2010; *Does facilitation by moss significantly affect performance and fecundity of a threatened endemic primrose?* (A. Rayburn); $800

Utah Native Plant Society Grant-in-Aid of Research

- 2010; *Does facilitation by moss significantly affect performance and fecundity of a threatened endemic primrose?* (A. Rayburn, J. Davidson, H. White); $1000

USU Ecology Center Research Grant

- 2008; *Hydraulic redistribution by* Artemisia tridentata*: a partial explanatory mechanism for clustered plant spatial patterns in sagebrush steppe communities?* (A. Rayburn); $4000

Leopold Center for Sustainable Agriculture Ecology Initiative Grant

- 2004-2006; *Using the past to plan the future: Retrospective assessment of landscape and land use change in the Clear Creek Watershed* (L.A. Schulte, A. Rayburn, L. Merrick); $14,998

Fellowships and Scholarships.

S. J. and Jessie E. Quinney Ph.D. Fellowship

- Utah State University; 2006 - present; $80,000 ($20,000 / yr over four years)

Merit-Based Scholarship

- Austin College; 1998-2001; $32,000 ($8,000 / yr over four years)

Awards.

Runner-up for Best Oral Presentation, Natural Resources Category

- 2010; *Using a chronosequence to link plant spatial patterns and ecological processes in grazed Great Basin semi-arid shrub-steppe communities* (Intermountain Graduate Research Symposium, Utah State University)

Utah State University Graduate Student Senate Travel Award

- 2010; Travel grant to attend the annual meeting of US Regional Association of the International Association for Landscape Ecology (US-IALE); $300

USDA-NIFA Professional Enhancement Award

- 2010; Travel grant to attend the annual meeting of US-IALE; $500

Urban – Rural Interfaces Student Award

- 2010; Travel grant to attend the Emerging Issues Along Urban - Rural Interfaces Conference; $575

Best Oral Presentation, Natural Resources Category

- 2009; *Spatial patterns and species interactions in a diverse Great Basin shrub community* (Intermountain Graduate Research Symposium, Utah State University)

Utah State University Graduate Student Senate Travel Award

- 2009; Travel grant to attend the annual meeting of US-IALE; $300

Teaching Assistant of the Year

- 2007; *Introduction to ArcGIS*, College of Natural Resources, Utah State University.

NASA-MSU Award in Landscape Ecology

- 2006; Travel grant to attend the annual meeting of US-IALE; $700

Refereed publications.

Rayburn, A.P., and A.L. Major. 2008. *Landscape history and baseline data collection inform the continuing restoration of a Midwestern prairie-savanna complex*. Journal of the Iowa Academy of Science 115:1-11.

Rayburn, A.P., and L.A. Schulte. 2009. *Integrating historic and contemporary data to delineate remnant natural areas within agricultural landscapes*. Natural Areas Journal 29: 4-14.

Rayburn, A.P., and L.A. Schulte. 2009. *Landscape change in an agricultural watershed in the U.S. Midwest.* Landscape and Urban Planning 93:132-141.

Rayburn, A.P., and M.V. Appledorn. 2010. *Prioritization of potential riparian buffer locations in an urbanizing, agricultural Midwestern (U.S.A.) watershed*. Proceedings of the 2010 Urban/Rural Interfaces Conference III:80-85.

O'Donnel, R.P. and A.P. Rayburn. 2011. *Biases in the protection of peripheral anuran populations in the United States*. Forthcoming in Herpetological Conservation and Biology 6(1).

Rayburn, A.P., Schiffers, K. J. and E. A. Schupp. 2011. *Use of precise spatial data for describing spatial patterns and plant interactions in a diverse Great Basin shrub community*. Plant Ecology 212:585–594.

Rayburn, A.P., and T.A. Monaco. 2011. *Using a chronosequence to link plant spatial patterns and ecological processes in grazed Great Basin plant communities*. Forthcoming in Rangeland Ecology and Management.

Rayburn, A.P. 2011. *Recognition and utilization of positive plant interactions may increase plant reintroduction success*. Biological Conservation doi:10.1016/j.biocon.2010.12.036.

Manuscripts in review.

Rayburn, A.P., J. Davidson and H.M. White. In review. *Facilitation by moss may significantly affect the distribution and performance of a threatened endemic primrose.* Oecologia.

Rayburn, A.P. and T. Wiegand. In review. *Spatial patterns of species diversity enhance understanding of community-structuring processes in a Great Basin, semi-arid shrubland*. Ecography.

Rayburn, A.P., J. Davidson and E. W. Schupp. In review. *Effect of storage time, site, and flower morph on germination of seeds of the threatened distylous primrose* Primula cusickiana *var.* maguirei. Plant Species Biology.

Wilson, T.L., A.P. Rayburn and T.C. Edwards Jr. In review. *Spatial ecology of*

burrow use by pygmy rabbits. Oikos.

Non-refereed publications.

Rayburn, A.P., H.W. White, and J. Davidson. 2011. The effect of facilitation by
moss on the distribution and performance of *Primula cusickiana* var. *maguirei.*
Sego Lily 34:6-8.

Presentations.

2011

- *Plant spatial patterns influence ecological processes in experimental semiarid
  grassland communities* (April 2011, US-IALE; Portland, OR)

- *Plant spatial patterns influence ecological processes in experimental semiarid
  grassland communities* (March 2011, Intermountain Grad. Research
  Symposium; USU)

- *Effect of storage time, site, and floral morph on seed germination of the
  threatened distylous primrose* Primula cusickiana *var.* maguirei (March 2011,
  Intermountain Grad. Research Symposium; USU)

- *Facilitation by moss may significantly affect the distribution and performance of a threatened endemic primrose* (Utah Rare Plant Meeting; Salt Lake City, UT)

- *Effect of storage time, site, and floral morph on seed germination of the threatened distylous primrose* Primula cusickiana *var.* maguirei (Utah Rare Plants; SLC, UT)

2010

- *Prioritization of potential riparian buffer locations in an urbanizing, agricultural Midwestern (U.S.A.) watershed* (Urban-Rural Interfaces; Atlanta, GA)

- *Using a chronosequence to link plant spatial patterns and ecological processes in grazed Great Basin semi-arid shrub-steppe communities* (US-IALE; Augusta, GA)

- *Spatial patterns of species diversity enhance understanding of community-structuring processes in a Great Basin, semi-arid shrubland* (Wildland Shrub Symposium.; USU)

- *Using a chronosequence to link plant spatial patterns and ecological processes in grazed Great Basin semi-arid shrub-steppe communities* (Intermountain Grad. Research Symposium; USU)

- *Prioritization of potential riparian buffer locations in an urbanizing, agricultural Midwestern (U.S.A.) watershed* (Intermountain Grad. Research Symposium; USU)

2009

- *Spatial patterns and species interactions in a diverse Great Basin shrub community* (Intermountain Grad. Research Symposium; USU)

- *Spatial patterns and species interactions in a diverse Great Basin shrub community* (US-IALE; Snowbird, UT)

2007

- *Forest change along an urban to rural gradient in an urbanizing Midwestern watershed (*Urban-Rural Interfaces; Atlanta, GA)

2006

- *Integrating ecological and social metrics of landscape change in Clear Creek watershed, Iowa (*US-IALE; San Diego, CA)

2005

- *Landscape Change in Clear Creek Watershed (IA)* (Natural Areas; Omaha, NE)

Posters.

2009

- *Spatial patterns and species interactions in a diverse Great Basin shrub community* (Ecological Society of America; Albuquerque, NM)

2004

- *Using the past to plan the future: retrospective assessment of landscape and land-use change in the Clear Creek watershed (Iowa)* (Special Initiative on Water Quality; Iowa State University, Ames, IA)

- *Using the past to plan the future: retrospective assessment of landscape and land-use change in the Clear Creek watershed (Iowa)* (World GIS Day; ISU, Ames, IA)

- *Suitability modeling for wetland restoration in Story County, Iowa: an exploration of weight tweaking and multiple model outputs* (World GIS Day; ISU, Ames, IA)

Teaching Experience.

University Co-instructor (Utah State University)**,** *Monitoring and Assessment in Natural Resource and Environmental Management* (Fall 2010). Responsible for design and implementation of lectures and labs in an upper-division class that emphasized synthesis of ideas, collection and analysis of ecological data, critical thinking and technical writing.

Graduate Teaching Assistant (USU)

- *Introduction to GIS Science* (Fall 2009)

- *Wetland Ecology and Management* (Spring 2009)

- *Wildland Ecosystems* (Spring 2007-2008)

- *Introduction to ArcGIS* (Fall 2006-2008)

Graduate Teaching Assistant (Iowa State University), *Ecological Methods* (2005)

Undergraduate Teaching Assistant (Austin College)

- *Cell Biology* (2000-2001)

- *Human Anatomy and Physiology* (2000-2001)

Guest Lectures

- "Plant propagation" in *Vegetation and Habitat Management* (Fall 2010), USU

- "Applications of survey-grade GPS in Ecology" in *Introduction to Geographic Information Science* (Fall 2009), USU

- "Wetlands and Watersheds"in *Wildland Ecosystems* (Spring 2009), USU

- "Western Wetlands" in *Wildland Ecosystems* (Spring 2007, 2008), USU

- "Soils, Topography, Relief" in *Ecology in a Changing World* (Spring 2007), USU

- "Seeds, Seedbanks, and Seed Fate" in *Restoration Ecology* (Spring 2007), USU

- "Landscape Ecology & Ecosystem Health" in *Concepts of Ecosystem Health* (Fall 2005), ISU

- "Introduction to FRAGSTATS" in *Landscape Ecol. and Nat. Res. Mgmt* (Spring 2005), ISU

Current Professional Activities.

- **Reviewer**: *Landscape Ecol.*, *Journal of Arid Environments*; *Journal of Vegetation Science*; *Landscape & Urban Planning*, *Journal of Basic & Applied Ecol., Arid Land Research & Mgmt.*

- **Member**: Ecological Society of America (ESA); International Association of Landscape Ecology (IALE), Scientific Research Society (Sigma Xi), National Forestry Honor Society (Xi Sigma Pi)

- **Advisor**: Clear Creek Watershed Enhancement Project (CCWEP), IA; Gombe School of Environment and Society (GOSESO), Tanzania, Africa

Past Professional Activities.

- Conference organizing committee, 2009 International Association of Landscape Ecology

- USU Ecology Center Seminar Selection Committee; 2007-2009

- Iowa State University Graduate and Professional Student Senate (GPSS); 2005-2006

- ISU GPSS Professional Advancement Grant (PAG) Committee; 2005-2006

- ISU Graduate Research in Ecology and Evolutionary Biology (GREBE); 2004-2006

- ISU Nat. Resource Ecology and Management Graduate Student Organization; 2004-2006

- ISU Student Chapter of the Society for Conservation Biology (2005)

Software Experience. R, ArcGIS, Programita (spatial analysis), MARXAN, GNSS Solutions (GPS), Adobe Photoshop, Macromedia Dreamweaver, SAS, Microsoft Office