Use of precise spatial data for describing spatial patterns and plant interactions in a diverse Great Basin shrub community

Andrew P. Rayburn · Katja Schiffers · Eugene W. Schupp

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 2,358 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.

Keywords Shrub spatial patterns · Facilitation · K2 · Great Basin semi-arid shrublands · GPS

A. P. Rayburn (✉) · E. W. Schupp
Department of Wildland Resources, and the Ecology Center, Utah State University, Logan,
UT 84322-5230, USA
e-mail: drew.rayburn@usu.edu

K. Schiffers
Department of Biological and Environmental Research,
University of Aberdeen, Aberdeen, Scotland, UK

Introduction

Processes that structure plant communities continue to be a primary focus of plant ecological research (Stoll and Prati 2001; Armas and Pugnaire 2005; Mokeny 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 and MacMahon 1981; Fowler 1986; Armas and Pugnaire 2005; Brooker et al. 2008; Mokeny 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 and MacMahon 1981; Tielbörger and Kadmon 2000; Schenk et al. 2003; Tirado and Pugnaire 2003; Armas and Pugnaire 2005). Although there are fewer experimental tests of the effect of spatial structure (Stoll and Prati 2001; Monzeglio and Stoll 2005), there is convincing evidence that intraspecific aggregation of plants in experimental communities can promote species coexistence (Stoll and Prati 2001; Monzeglio and Stoll 2005; Mokeny 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 and 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 and Woodell 1973; Phillips and MacMahon 1981; Skarpe 1991). Random patterns may be a direct result of ecological processes such as habitat heterogeneity (Tirado and Pugnaire 2003), or may emerge temporarily when aggregated patterns shift to regular patterns because of density-dependent mortality (Prentice and 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 and MacMahon 1981; Eccles et al. 1999; Tirado and 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 et al. 1996; Armas and 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 and 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 et al. 2004; McIntire and 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 and 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.

In general, 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 and MacMahon 1981), progressive mapping (Rohlf and 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 and 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 ≥ 1 m that may render inappropriate any fine-scale (e.g. <1 m)

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 et al. 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 obtain 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 and 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 39 m by 39 m 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 1 s 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 5 s with a 1 s 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).

Data analysis

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 and 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 and 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 and Moloney 2004), and in contrast to Ripley's K, the K2 is non-cumulative; 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 and 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 (Loosmore and Ford 2006; Blanco et al. 2008). This

is less of a concern when using non-cumulative statistics (Loosmore and 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 and 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 non-cumulative 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 and 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 identify of 2,358 individual shrubs within the study plot (Fig. 1). Data collection required approximately 16 field hours, with data-post processing requiring an additional 1–2 h. 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/m², while densities of individual shrub species ranged from 0.19 to 0.61 shrubs/m² (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 <0.50 m, 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 <0.50 m (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 0.10 m < r < 0.25 m and r = 0.50 m, respectively; Fig. 2c, d). 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 the 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

Data collection and analysis

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

Fig. 1 Map of study plot (39 m × 39 m), showing locations of all shrub individuals (*upper left*) and maps detailing the locations of individuals from each of the five shrub species
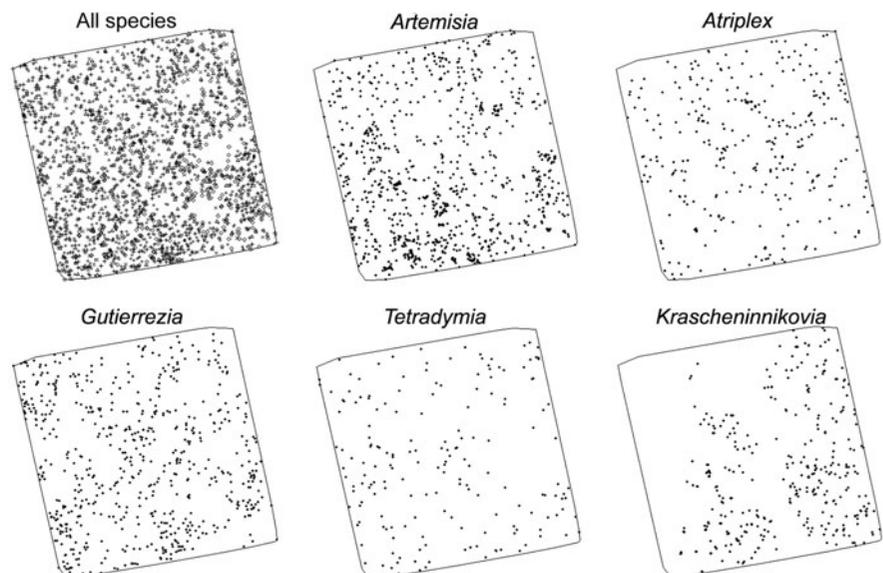
Table 1 Summary statistics for shrub spatial data by taxon

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

$N_{species}$ = sample size per species; proportion = % of total; $\lambda_{species}$ = density (shrubs/m^2); N_{total} = 2,358

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 USA. Although past authors have provided convincing evidence of statistically significant plant spatial patterns, larger and more precise datasets could lead to more convincing 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.
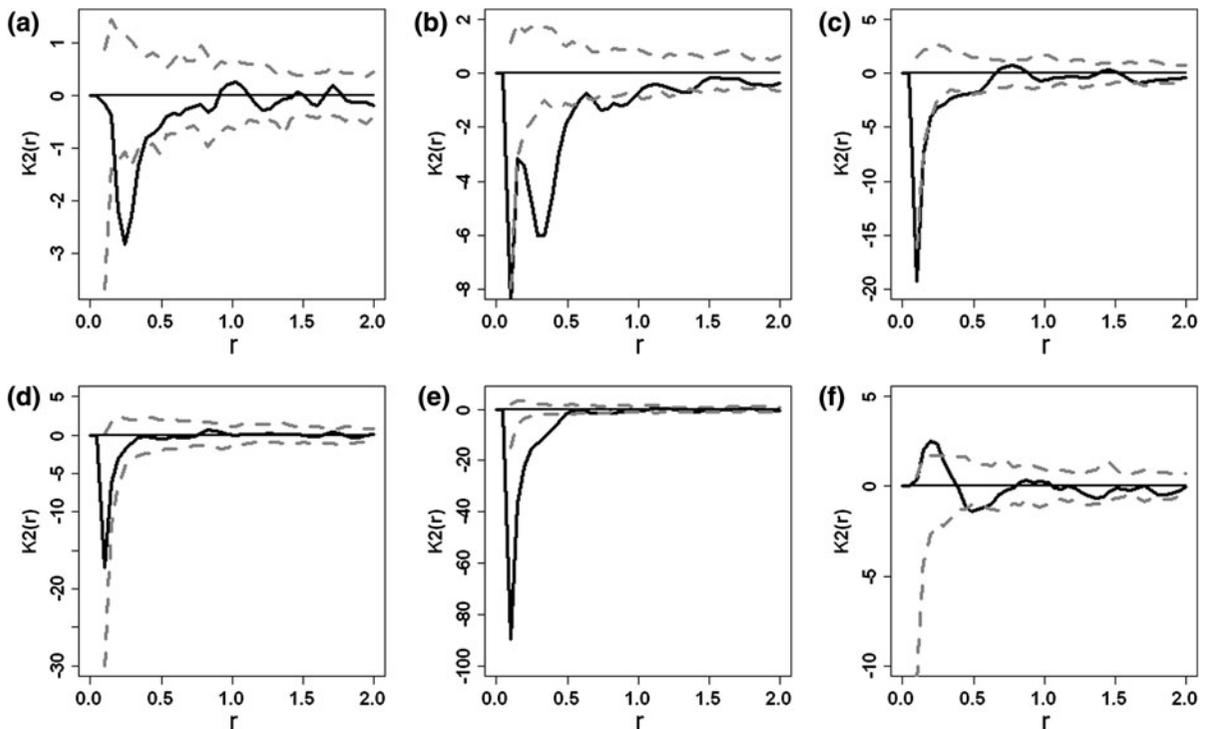
Fig. 2 K2 plots for **a** all species combined; **b** *Artemisia tridentata*; **c** *Atriplex confertifolia*; **d** *Krascheninnikovia lanata*; **e** *Gutierrezia sarothrae;* and **f** *Tetradymia canescens. Dotted lines* indicate 95% Monte Carlo simulation envelopes (N_{sim} = 199). Significant aggregation 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
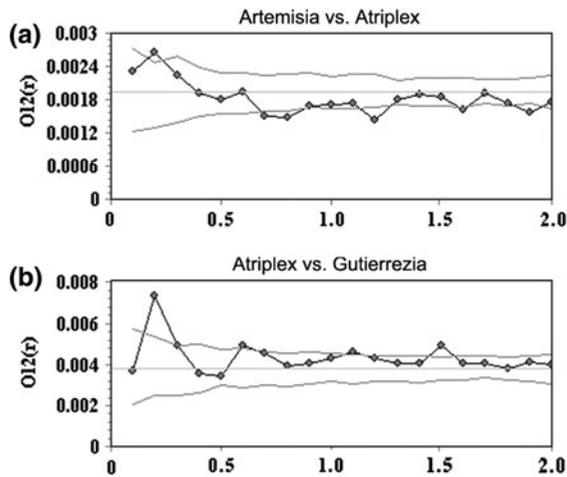
Fig. 3 Plots of bivariate O-ring statistics for two species pairs with significant spatial structure; **a** *A. tridentata* relative to *A. confertifolia*; **b** *A. confertifolia* relative to *G. sarothrae*. Values of x-axis are in 0.1 m increments. *Gray lines* are 95% Monte Carlo simulation envelopes (N_{sim} = 199). Both plots show significant aggregation of shrub species pairs at a distance of approximately 0.20 m (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

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 represent 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 and 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 and 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 extremely 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 and 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).

Finally, 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 and 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 and 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 conspecifics 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 and 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 PB, Raff DA, Laurenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Armas C, Pugnaire FI (2005) Plant interactions govern population dynamics in a semi-arid plant community. J Ecol 93:978–989

Baddeley AJ, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. J Stat Softw 12:1–42

Blanco PD, Rostagno CM, del Valle HF, Beeskow AM, Wiegand T (2008) Grazing impacts in vegetated dune fields: predictions from spatial pattern analysis. Rangel Ecol Manag 61:194–203

Boose ER, Boose EF, Lezberg AL (1998) A practical method for mapping trees using distance measurements. Ecology 79:819–827

Brooker RW et al (2008) Facilitation in plant communities: the past, the present, and the future. J Ecol 96:18–34

Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecol Appl 10:1400–1413

Eccles NS, Esler KJ, Cowling RM (1999) Spatial pattern analysis in Namaqualand desert plant communities: evidence for general positive interactions. Plant Ecol 142:71–85

Elmore FH (1976) Shrubs and trees of the Southwest Uplands. Southwest Parks and Monuments Association, Tucson

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

Fowler N (1986) The role of competition in plant communities in arid and semi-arid regions. Annu Rev Ecol Syst 17:89–110

Franco AC, Nobel PS (1988) Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. Ecology 69:1731–1746

Freeman EA, Ford ED (2002) Effects of data quality on analysis of ecological pattern using the K(d) statistical function. Ecology 83(1):35–46

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

HilleRisLambers R, Rietkerk M, Van den Bosch F, Prins HTH, De Kroon H (2001) Vegetation pattern formation in semi-arid grazing systems. Ecology 82:50–61

Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, de Ruiter PC (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213–217

King TJ, Woodell SRJ (1973) The causes of regular pattern in desert perennials. J Ecol 61:761–765

Lavine A, Gardner JN, Reneau SL (2003) Total station geologic mapping: an innovative approach to analyzing surface-faulting hazards. Eng Geol 70:71–91

Loosmore NB, Ford ED (2006) Statistical inference using the G or K point pattern spatial statistics. Ecology 87:195–1931

MacMahon JA (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 EJB, Fajardo A (2009) Beyond description: the active and effective way to infer processes from spatial patterns. Ecology 90:46–56

Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. J Ecol 94:973–979

Mokeny 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

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

Prentice IC, Werger MJA (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. http://www.R-project.org

Rebollo S, Milchunas DG, Noy-Meir I, Chapman PL (2002) The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. Oikos 98:53–64

Rohlf FJ, Archie JW (1978) Least-squares mapping using interpoint distances. Ecology 59:126–132

Schenk HJ, Holzapfel C, Hamilton JG, Mahall BE (2003) Spatial ecology of a small desert shrub on adjacent geological substrates. J Ecol 91:383–395

Schiffers K, Schurr FM, 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

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043–1048

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 Appl 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. Ecology 82:319–327

Strand EK, Vierling LA, Smith AM, Bunting SC, Hann DB, Gessler PE (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. Ecology 81:1544–1553

Tirado R, Pugnaire FI (2003) Shrub spatial aggregation and consequences for reproductive success. Oecologia 136: 296–301

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

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

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

Wiegand T, Kissling WD, Cipriotti PA, Aguiar MR (2006) Extending point pattern analysis to objects of finite size and irregular shape. J Ecol 94:825-837