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# Soil patchiness in juniper-sagebrush-grass communities of central Oregon

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**Abstract**

This study compared the sizes, spacings and properties (soil moisture, pH, nitrogen, soil arthropods and VAM) of soil resource islands and bare patches in sagebrush-grass communities invaded by western juniper versus those without juniper. We analyzed 1000 surface soil samples taken from nine 50-m radius circular plots sampled in December of 1991 and May of 1992 on 'The Island', one of the few undisturbed areas of sagebrush-grass shrubland in Oregon. Spatial structure was interpreted from correlograms (Moran's I) and standardized semivariograms. The presence of juniper was associated with increased bare area and smaller, more widely spaced grass and sagebrush plants. Soil arthropod numbers and biomass in plots with juniper were only roughly one-fifth of those in sagebrush-grass plots in December. The dominant soil pattern in both sagebrush-grass and juniper-sagebrush-grass plots was regularly-distributed patches spanning a range of sizes and spacings. Plots with juniper had greater patchiness at shorter lags (<3 m), and patchiness was more developed for soil moisture, net nitrification, and net N mineralization, whereas sagebrush-grass plots had greater patchiness at longer lags (3 – 9 m) and patchiness was more developed for $NO_3$–N, arthropod numbers and biomass. These differences in soil patterns with and without juniper indicate that juniper responds to, or causes, changes in the size of resource islands under sage and grass when it invades sage-grass communities.

## Introduction

Recent studies in ecology have emphasized the need to understand influences of patterns upon processes (Turner, 1989); the importance of scale in determining perceived patterns (Levin, 1992); and the spatial interactions of community-level processes such as competition and nutrient transfer (Polis et al., 1997). In plant communities, patterns of vegetation spacing and arrangement and associated soil patches may interact with nutrient cycling processes and community dynamics at multiple scales. We hypothesize that the invasion of western juniper (*Juniperus occidentalis Hook.*) in sagebrush-grass communities in central Oregon is associated with a change in the sizes and arrangements of plants and associated soil resource islands under sagebrush and grass.

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Nutrient cycling in soils of sagebrush-grass communities involves interactions among arthropods and fungi, but studies of soils under sagebrush (Charley and West, 1975; Halvorson et al., 1994, 1995, 1997) have focused on nutrients, moisture and microbes, with little emphasis on arthropods or fungi. Juniper, sagebrush and the common perennial grasses all form mutualistic associations with vesicular-arbuscular mycorrhizal (VAM) fungi, and these increase the efficiency of the host plant to sequester soil nutrients (Trappe, 1981). Soil fauna contribute to initial decomposition and nitrogen mineralization (Santos et al., 1981; Whitford, 1986) but are sensitive to litter quality and microclimate (Wallwork, 1976). Soil arthropods also may influence nutrient cycling patterns via selective feeding on decomposer fungi or microbes, while the fungivorous micro-and macro-arthropods may influence VAM fungi by consuming hyphae and spores (Ingham et al., 1985; Rabatin and Skinner, 1985).

Many studies have quantified spatial patterns in soils of sagebrush-grass communities, but the processes that produce these patterns are less clear. Sagebrush-grass communities lend themselves to studies of soil patterns because the near-regular spacing of plants and bare areas produce simpler patterns than plant communities with higher cover (e.g. Torgerson et al., 1995). Soils under both sagebrush and perennial grasses are characterized by distinct patches, called 'resource islands', which have higher nitrogen and moisture than bare areas (Charley and West, 1975; Halvorson et al., 1994, 1994, 1997; Hook et al., 1991, 1994; Jackson and Caldwell, 1993 a, b; Smith et al., 1994). Soil resource islands associated with vegetation occur in many arid systems, but the processes that form them are not well understood (Belsky et al., 1993; Padien and Lajtha, 1992; Ryel et al., 1996; Schlesinger et al., 1990, 1996). Resource islands could be the result of spatial redistribution of material on the soil surface e.g. by water or wind (Schlesinger et al., 1996), or they could involve litterfall, decomposition, and nutrient cycling processes in the root zone (Hook et al., 1994). Little is known about how long it takes to create or modify soil resource islands, although Ryel et al. (1996) found that their strength of expression varied by season, and Halvorson et al. (1997) found elevated levels of soil C and N near charred stumps of sagebrush nearly a decade after fire.

The big sagebrush-bluebunch wheatgrass communities of central Oregon have undergone an increase in the establishment of western juniper (*Juniperus occidentalis Hook.*) since the turn of the century (Eddleman, 1987). This tree is regarded as a weed of rangelands by cattle ranchers because it appears to result in a reduction of forage, both of big sagebrush (*Artemisia tridentata)* and the native perennial grasses (*Agropyron spicatum*, *Poa secunda*, and *Festuca idahoensis*) (Belsky, 1996). The expansion of juniper may be due to fire suppression, livestock grazing, enhanced tree growth rates associated with increases in atmospheric $CO_2$ (Belsky, 1996; Eddleman, 1987; Knapp and Soule, 1996), or other factors.

The spatial process of juniper invasion in sage-grass communities tests the dynamics of resource islands. Juniper may be able to interact with roots and soil resource islands under adjacent sagebrush and grass clumps, because it has a much deeper tap root and a more extensive surface root system than sagebrush, allowing it to exploit soil resources several meters from the tree (Flanagan et al., 1992; Kramer et al., 1996; Miller et al., 1987). Juniper may preferentially invade certain sizes and spatial patterns of bare patches in sage-grass communities: weedy invaders traveled farther (invaded more successfully) in experimental systems whose bare areas were large and uniformly spaced (Bergelson et al., 1993).

We propose that juniper invasion in sagebrush-grass communities involves interactions among extensive roots of juniper with those of sagebrush and grass, affecting the sizes and spacing of plants, soil resource islands and bare patches. We tested the hypothesis that the presence of juniper is associated with changes in soil properties and sizes of resource islands in juniper-sagebrush-grass communities.

## Methods

### *Study site*

The influence of juniper invasion upon, or its response to, soil spatial patterns was assessed by comparing plots that had juniper or lacked juniper for several decades in an otherwise homogeneous, undisturbed, flat, isolated site in central Oregon. Our study area was an approximately 0.25 $km^2$ portion of 'The Island' (44° 34′ N, 121° 16′ W), a 0.78 $km^2$ mesa emerging from the southern edge of Lake Billy Chinook, in the Palisades State Park, Central Oregon (Figure 1). The study site was selected because it contains sagebrush-grass communities with and without juniper, is one of the few areas of central Oregon that has been undisturbed by domestic livestock grazing, and has relatively few exotic species. The Island has an elevation of 731 m above sea level, and rises 139 m above the lake which borders all but its southernmost edge. The lake was created by damming of the Deschutes and Crooked rivers in 1963.

The climate of the Island is xeric with warm dry summers and cool wet winters. Mean monthly temperatures at Madras, approximately 15 km to the northeast of The Island, range from –1.3 °C in January to 19.2 °C in July. A minimum temperature of –42.8 °C and a maximum of 44.4 °C have been recorded. Mean annual precipitation at Madras is 236 mm, 88% of which falls as snow or rain between October and June. Frosts can occur during any month of the year, but are less likely during June, July and August (Driscoll, 1964).

The Island's geology consists of 10 000 to 15 000 year old basaltic flows interspersed with volcanic ash deposits. The soil parent material is unconsolidated

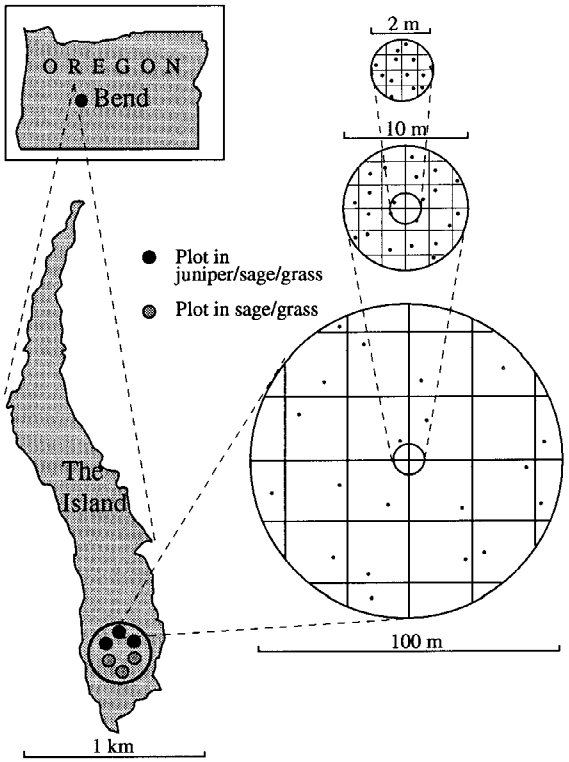


*Figure 1.* Study site location and sampling design for study of spatial patterns of soil biological and chemical properties under sagebrush-grass and juniper-sagebrush-grass communities in central Oregon. Plots were located at the southern tip of The Island at a transition from juniper-sagebrush-grass to sagebrush-grass. Fifty-two soil samples were obtained in each of nine 50-m radius (0.79 ha) plots centered on or close to clumps of grass. Three plots were sampled in December 1991; two in the sagebrush-grass and one in the juniper-sagebrush-grass communities. Six plots were sampled in May 1992; three each in the sagebrush-grass and juniper-sagebrush-grass communities. Each plot contained three nested randomized grid subplots. The innermost 1-m radius subplot contained 12 points in a 0.5 m grid; the middle 5-m radius subplot contained 20 points in a 2 m grid, and the outermost 50-m radius subplot contained 20 points in a 20 m grid. The inner 1-m radius subplot covered an area of bare soil and grass, the 5-m radius subplot covered an area of bare soil with grass clumps and sagebrush, and the outermost 50-m radius plot covered an area of bare soil, grass clumps, sagebrush and, in juniper-sagebrush-grass plots, several juniper trees. Semi-variances and autocorrelation coefficients for 0 – 2 m lags describe patterns in the central 1-m subplot, those for 0 – 10 m lags describe patterns in the central 5-m subplot, and those for 10 – 30 m lags describe patterns contrasting the inner and outer subplots.

lake sediments laid down before the Deschutes and Crooked rivers cut the canyons that now surround the site (Driscoll, 1964). The subsequent Mazama eruption 8000 years ago and later Newberry crater eruptions may also have contributed ash deposits to the site. The soils are classified as Typic and Lithic Cryorthents and tend to be shallow with basaltic rocks at the surface (Leighty, 1958).

Vegetation on the Island consists predominantly of *Juniperus occidentalis* (western juniper), *Artemesia tridentata* (sagebrush), *Agropyron spicatum* (bluebunch wheatgrass) and *Poa sandbergii* (sandberg bluegrass), with some *Pershia tridentata* (antelope bitterbrush), *Festuca idahoensis* (Idaho fescue) and *Bromus tectorum* (cheatgrass). Knapp and Soule (1996) repeated Driscoll's (1964) survey in the juniper-sagebrush-grass community on the Island and documented increases in juniper (from 5 to 10% cover) and sagebrush (from 9 to 16% cover), no change in cover of *A. spicatum* (9%), *Poa spp.* (1–2%), or *F. idahoensis* (0.5%), and a decline in *B. tectorum* from 1.7 to 0.1% cover from 1960 to 1994. The Island is relatively undisturbed because it is inaccessible to vehicles and cattle, but a few sheep grazed there in the 1920s (Driscoll, 1964). Deer, rabbits and ground squirrels are now the main mammalian herbivores.

### *Sampling design*

The study site examined in detail (Figure 1) was a level area of approximately 0.25 km$^2$ supporting a vegetation of predominantly sagebrush and perennial grasses. Junipers have been encroaching gradually upon this area from the north over the past few decades. A total of nine 50-m radius circular plots were sampled, three in December of 1991, and six in May of 1992. In each 50-m plot, 52 random non-aligned sampling points were arranged in three concentric nested circular subplots (Figure 1). This nested spatial design was used to characterize the plot and test for autocorrelation at three spatial scales.

### *Field data collection*

Vegetation composition for each plot was estimated by the point-intersection method. At each sampling point, the type of plant cover was recorded, surface litter was removed, and a soil core and bulk sample were taken. The soil core (10 cm diameter and 5 cm depth) was taken for microarthropod extraction, and the bulk sample (approximately 500 g of soil to a depth of 5 cm) was taken from the area immediately surrounding the core for chemical analysis. Soil samples were transferred within one day to a cool room at 4 °C, where they were stored at field moisture until laboratory analysis (Bartlett and James, 1980).

Spacing between sagebrush and juniper plants was determined by mapping all sagebrush or juniper loc-

ations in randomly-located circular plots of 15-m radius (sagebrush) or 50-m radius (juniper). Nearest-neighbor distances between grass clumps were determined in three 3×3 m square plots. Sagebrush and grass spacing were determined in both the juniper-sagebrush-grass and sagebrush-grass communities.

*Laboratory analyses*

Soil arthropods were extracted from the 10 cm diameter cores using a MacFayden high gradient extraction funnel over a 14 day period (Freckman et al., 1986; Merchant and Crossley, 1970). Samples taken in May 1992 were humidified to break drought-induced dormancy in the soil fauna by adding approximately 3 mL of distilled water to each polythene bag with a plant mister prior to cool storage (A. Moldenke, pers. comm.). Arthropod extractions were begun within 3 days of sample collection. Numbers of each species were noted for each sample and were grouped into guilds based on diet (Roberts, 1994).

Root infection by vesicular-arbuscular mycorrhizal fungi was assessed from stained root samples under a dissecting scope using a grid intersection method (Giovannetti and Mosse, 1979). Roots of diameter 0.5–1 mm remaining on a 2-mm sieve were stored in tap water in 'Tissue Tek' capsules at 4 °C for up to 3 days prior to staining. Roots were cleared in hot 10% KOH solution for 0.5 – 1.5 h in a steamer, neutralized in 1% HCl, stained with trypan blue (Phillips and Hayman, 1970), then de-stained and stored in lactoglycerin. VAM infection was expressed as a percentage of the total root-grid intersections. Replicated assessments of 20 randomly selected samples indicated that this technique had approximately a 10% error. VAM infection percent was estimated for the entire soil sample because roots could not be identified to species (C. Roberts, unpublished data).

Chemical analyses were carried out on the < 2-mm diameter fraction of soil at field moisture content; results were expressed per gram of oven dry soil. Soil moisture was determined gravimetrically. Soil pH was determined with a glass electrode (Corning, model no. 215) on a 25 g sample in a 1:2 soil:water ratio by weight. Net nitrogen mineralization was determined using 14-day incubations following the aerobic incubation technique (Anderson and Ingram, 1989). Short term incubations produce results comparable to those from longer incubation periods (Stanford and Smith, 1972; Stanford et al., 1974). Initial $NH_4$–N and $NO_3$–N were extracted with 2N KCl using a 1:5 soil:KCl ratio. The extracts were assayed for nitrogen content on an auto-analyzer (Alpkem R.F.A. model no. 300) using an Indophenol assay for $NH_4$–N and a cadmium reduction assay for $NO_3$–N (Keeney and Nelson, 1982; EPA-600/4-79-020). Net nitrogen mineralization was determined as the sum of the differences in pre- and post-incubation concentrations of $NO_3$–N and $NH_4$–N. December samples were incubated at field moisture. May samples were brought to December field moisture content (approximately 25%) by the addition of distilled water introduced with a plant mister while gently shaking the soil to achieve crumb formation. This method helped retain an aerobic soil structure. Variability introduced by storage of the samples was distributed throughout the samples by analyzing them in random order.

*Parametric statistical analyses*

Data for each soil property were analyzed using the SYSTAT statistical package (Wilkinson et al., 1996). Data were checked for independence, normality and equality of variance prior to statistical analyses. The spatial statistical analysis (below) indicated that only sampling points beyond 10–15 m of one another were independent, so comparisons of whole plots used only the sampling points in the largest nested subplot ($n$=20), separated on average by 20 m. However, all data points were used in the analysis by vegetation cover type in order to capture the effects of rare cover types (e.g. juniper). All variables except VAM were log-normally distributed, and these were transformed using a $\log_e$ transformation.

Each sampling point was classified according to its plant cover (bare soil, grass, sagebrush and juniper). Each plot was classified by season (December, May) and by community type (sagebrush-grass, juniper-sagebrush-grass). For each soil property two ANOVAs were conducted: 1. a one-way analysis with plant cover as the treatment factor, and 2. a 2×2 factorial analysis with season and community type as the treatment factors. When more than one pairwise comparison was tested, probabilities were conservatively adjusted using Tukey's highest significant difference test to guarantee an overall protection of $\alpha$ = 0.05 (Neter et al., 1990; Steel and Torrie, 1980; Wilkinson et al., 1996).

*Spatial statistical analyses*

The spatial structure and spatial autocorrelation for each soil property within each plot were examined

using correlograms (Moran's I) and standardized semivariograms (Cressie, 1993, Legendre and Fortin, 1989; Rossi et al., 1992). Correlograms were tested for significance following Sokal and Oden (1978). A total of 90 correlograms and 90 semivariograms (ten soil properties in each of nine plots) were constructed using observed data, and an additional 20 of each were constructed simulated data. Calculations were performed using a C program on a SUN workstation using $n$=30 pairs of points for each semivariance and spatial autocorrelation coefficient, and semivariogram and correlogram shapes were examined at lags up to 25 m. Following Rossi et al. (1992), changes in local means and variances (non-stationarity) were accounted for by selective removal of outliers, data transformations, and removal of trends.

Spatial structures were interpreted from positive and negative significant values of Moran's I in correlograms (shown conceptually in Figure 2). Values of Moran's I usually range between –1 and +1, but can exceed these limits when outliers are present. A positive value of Moran's I indicates that points at a given lag on average are more similar to each other than to the overall mean, while a negative value of I indicates differences among points at a given lag that on average are greater than their differences to the overall mean (Figure 2). In the example in Figure 2, the significant positive Moran's I at 0.5 – 1 m could be interpreted as a measure of the minimum patch size. The negative correlations at 1.5 m – 2 m lags in Figure 2 can be interpreted as approximately half the pattern wavelength (pairs A–D, D–F, F–G) or the distance between the center of the patch and the center of the interpatch space. The positive significant values of Moran's I at 2.5 and 6 m in Figure 2 can be interpreted as a full wavelength or the distance between successive patch centers (pairs A–F or D–G) (Legendre and Fortin, 1989). It is correct to interpret patch size and space size from a correlogram as described above only when the pattern consists of regularly distributed patches covering roughly 50% of the sampled area, i.e. a sine wave in one dimension or an egg carton in two dimensions (Errington, 1973).

Spatial structures also were interpreted from standardized semivariograms based on the nugget variance, the range and the sill (Burgess and Webster, 1980; Burrough, 1983b; Rossi et al., 1992). The standardized semivariance and the spatial autocorrelation coefficient are inversely related (Rossi et al., 1992), so standardized semivariograms were expected to corroborate structures in correlograms. Ecological data often produce semivariograms with positive nuggets, multiple ranges and sills at short lags, indicative of patchy patterns. The nugget is the semivariance at the shortest distance between samples. A positive nugget is a measure of unexplained between-sample variance, error introduced during sampling or analysis or structure below the minimum between-sample distance (Rossi et al., 1992). The range is the distance at which points cease to be autocorrelated, and the semivariance reaches a plateau or declines (Burgess and Webster, 1980). A semivariogram with multiple ranges is indicative of a repeating pattern, and the successive peaks may indicate multiple scales of pattern in the data (Burrough, 1983b; Legendre and Fortin, 1989) or the lag harmonics of a single scale of pat-

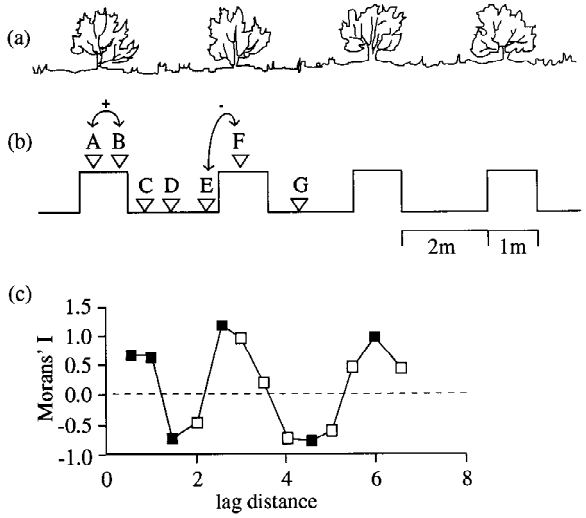


*Figure 2.* Approach to the study of soil spatial pattern using spatial autocorrelation. Regularly-spaced plants such as grass clumps, sagebrush or juniper trees (a) should produce corresponding peaks and troughs in soil properties (b) which are detectable using spatial autocorrelation analysis such as a correlogram (c). The correlogram shows how the levels of the soil property in (b) are autocorrelated as a function of the distances between pairs of sampling point (A–G). Solid squares indicate significant values of Moran's I ($p$<0.05). Pairs of similar values such as A–B or C–D are more frequent at <1 m lag than pairs of dissimilar values like B–C, producing significant positive Moran's I values at this lag which represent the sizes of sage clumps (1 m) or bare patches (2 m). Frequent pairs of similar values such as A–F, B–F, C–G, D–G, E–G produce a significant positive Moran's I at 2.5 m lag reflecting the average spacings between sage clumps (2 – 4 m), and between bare patches (1 – 5 m). A negative value of Moran's I results when the frequency of dissimilar pairs of points exceeds that of similar pairs at a given lag distance. Pairs such as A–C, A–D, A–E, B–C, B–D, B–E produce a negative Moran's I at 1.5 m reflecting the average spacing between sage clumps and adjacent bare patches (0 – 4 m) while pairs such as A–G, B–G produce a negative Moran's I at 4.5 m reflecting the average spacing between sage clumps and the next nearest bare patches (3 – 6 m).

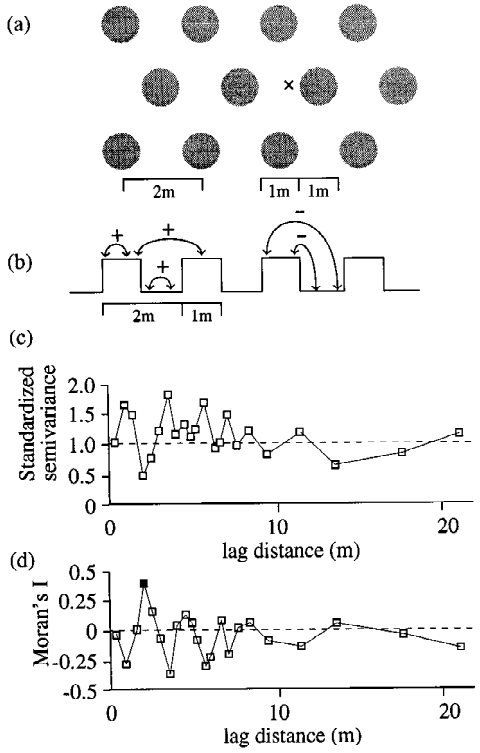


*Figure 3.* Results of spatial pattern analysis on simulated regular landscape (design 1, Table 1) showing the limit of our sampling design to detect certain patterns. The simulated landscape (a, X indicates plot center) represents 1-m diameter sagebrush (grey circles) regularly spaced at 2-m intervals, similar to the sizes and spacings we observed in sampled sagebrush-grass plots. Hypothesized levels of a soil property along a transect through this landscape (b) show fluctuations corresponding to bare areas and plant canopies, with arrows displaying expected sign (+ or –) of Moran's I autocorrelation coefficient within and between patches. This fine-scale pattern was poorly detected by our sampling design: the standardized semi-variogram (c) shows a pattern indistinguishable from random, while the correlogram (d) shows one significant positive value of Moran's I which could be expected by chance. Therefore, we assumed our design was detecting a regular pattern at this scale only if autocorrelations at similar lag distances occurred for more than one soil property in a given plot or in more than one replicate plot for a given soil property.

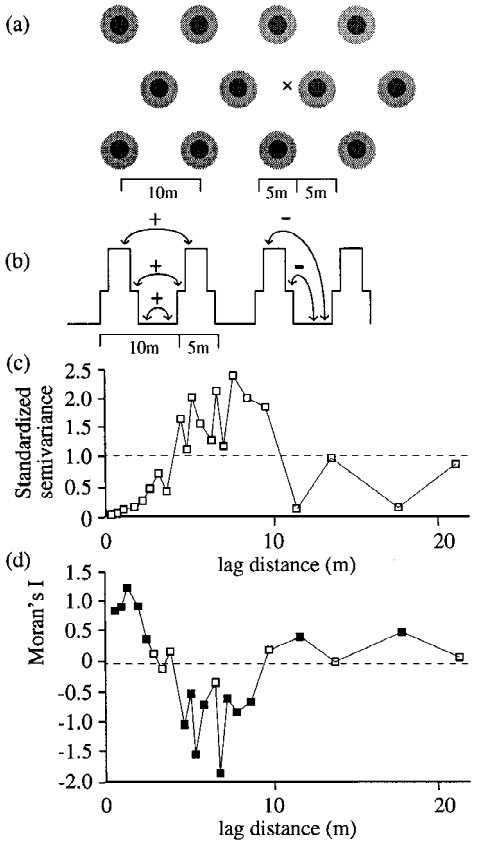


*Figure 4.* Results of spatial pattern analysis on simulated regular landscape (design 5, Table 1), showing ability of our sampling design to detect certain patterns, but limited ability to accurately detect size and spacing. The simulated landscape (a) contains 2.5-m diameter junipers (dark grey circles) with 5-m diameter root crowns (grey circles) regularly spaced at 10 m intervals, similar to the sizes but slightly more closely spaced than those we observed in juniper-sagebrush-grass plots. Hypothesized levels of a soil property along a transect through this landscape (b) show fluctuations corresponding to bare areas, root crowns and plant canopies, with linked arrows displaying expected sign (positive or negative) of Moran's I autocorrelation coefficient within and between patches. This landscape pattern, and designs 3, 4, 6, 7 and 8, were clearly detected by our sampling design: the standardized semi-variogram (c) shows a pattern of steadily increasing semivariance up to a range of 5–10 m, while the correlogram (d) shows five significant positive values of Moran's I at lags below 3 m, and 8 significant negative values of Moran's I at lags from 3 to 8 m, much more than expected by chance. Patch sizes and spacings interpreted from this correlogram give slightly biased averages of true patch sizes: the interpreted patch size is 3 m or less when in fact it was 2.5 – 5 m, while the interpreted patch-interpatch spacing is 3 – 8 m when in fact it was 0 – 10 m.

tern (Cohen et al., 1990). The sill is the maximum semivariance observed within the semivariogram. The sill is expected to occur at long lags (semivariogram has a positive slope), but when it occurs at a short lag (part of the semivariogram has a negative slope), this indicates patchiness, i.e. samples close to each other are more different than those farther apart.

Removal of outliers strongly influenced our ability to discriminate genuine spatial structures in these data, but non-normality of data was not problematic, and anisotropy was absent. Single outliers (defined as observations outside the inner fences, or plus or minus 1.5 times the interquartile range (Wilkinson et al., 1996), these represented <2% of data points) were removed in 31 of 90 cases. Comparison of correlo-

grams before and after removal of outliers revealed structures previously suppressed or corroborated the existence of spatial structures unaffected by outliers (Roberts, 1994). Even with a fairly large number of pairs of points used to calculate each semivariance or autocorrelation coefficient (we used 30 following Legendre and Fortin (1989)), single outliers at given lag distances inflated Moran's I so much that autocorrelations representative of true structure at other lag distances appeared to be insignificant. After one or two outliers per plot had been removed, some variables remained highly skewed, but even for these variables normalizing the data had no appreciable effect on semivariogram shape. No underlying trends in these datasets (anisotropy) were detected (Roberts, 1994).

*Limits of detection of spatial pattern*

Spatial analysis techniques may fail to detect random patterns or regular patterns which are very sparse or very dense (Errington, 1973). To determine whether the sampling design and spatial statistical analyses in our study could detect spatial pattern, the sampling design was applied to simulated landscapes. Eight simulated landscapes were regularly-patterned, corresponding to the sizes and spacings of *Artemesia* shrubs and *Juniperus* trees observed in the study site, and a further 10 simulated landscapes were random, one for each sampled soil property (Table 1). Simulated landscape designs were developed to test the ability of the analysis method to detect regular patterns of canopy cover ranging from 1 to 50% with root areas ranging from 2 to 100%. Designs 1, 2 and 3 were based on the size and spacing of sagebrush, small junipers and large junipers in the study area. Designs 4 to 8 tested intermediate combinations of vegetation size, spacing, canopy cover and root areas. The sampling design (Figure 1) was overlaid on each of the 8 regularly patterned simulated landscapes, and arbitrary values of 1, 2 and 3 plus or minus a random number between 0 and 0.02 were assigned to sampling points falling on bare soil, root zone, and canopies, respectively. In Design 9, numbers drawn at random from a distribution constrained by the range (minimum, maximum) and shape (normal, log-normal) of the observed data for each of the ten soil properties were assigned to each of the sampling points, producing 10 simulated random landscapes. Each of the 18 simulated landscapes was then evaluated using the same spatial statistical analyses as the field-measured data (Roberts, 1994).

Our use of simulated landscapes permitted us to discriminate genuine from spurious spatial structures in the observed data, and to ascertain the limits of our sampling design. The simulated random landscapes helped us to identify significant values of Moran's I occurring purely by chance in correlograms constructed from observed data. We used a 95% confidence interval to determine the significance of each of the 25 values of Moran's I in our correlograms (Sokal and Oden, 1978) rather than correcting for the multiple tests performed in each correlogram (Legendre and Fortin, 1989). The random landscapes showed fewer significant correlations than expected by chance: five of the 11 correlograms created from random data showed one significant correlation each, and one correlogram showed two significant correlations; six of these seven spurious significant correlations were at lags below 10 m.

Simulated regular landscapes helped us to determined which of a range of hypothetical regular patterns could really be detected by our sampling design, and which could not. Our sampling design was unable to reliably detect pattern in a single-plot simulated landscape with plant size and spacing representative of the sagebrush-grass community (design 1, Table 1; Figure 3). Therefore, we assumed our design was detecting a regular pattern in observed soil properties in the sagebrush-grass community only if several plots showed autocorrelations at similar lag distances. However, for simulated landscapes with as little as 1% canopy cover in the juniper-sagebrush-grass community (Table 1, designs 2 – 8), our sampling design produced semivariograms with a distinct shape compared to those from random landscapes and correlograms with four or more significant values of Moran's I, much more than the 1.25 expected by chance alone (e.g. design 5, Figure 4).

Simulated regular landscapes also revealed how accurately we could detect patch size and spacing in observed data. The sampling design and spatial analysis techniques were able to accurately detect patch size and spacing in the regularly patterned landscapes only when cover approached 50% (e.g. design 5, Figure 4). Patch sizes inferred from correlograms constructed from the regularly patterned simulated landscape designs 3 – 8 (Table 1, Figure 2) overestimated the actual size of 1 and 2-m canopies and bare patches, but underestimated the actual size of 2.5 – 5-m canopy, root crown and bare patches. The most severe discrep-

*Table 1.* Simulated landscape designs used to test the ability of the analysis method to detect regular patterns of canopy cover ranging from 1 to 50% with root areas ranging from 2 to 100%

| | Juniperus | | | Artemesia | | Approximate cover of | | |
|---|---|---|---|---|---|---|---|---|
| Deisgn | Spacing (m) | Canopy diameter (m) | Root crown diameter (m) | Spacing (m) | Canopy diameter (m) | Rootless area (%) | Canopy (%) | Root crown (%) |
| 1[a] | - - | - - | - - | 2 | 1 | 61 | 39 | 39 |
| 2 | 18 | 1 | 2 | - - | - - | 98 | 1 | 2 |
| 3 | 18 | 5 | 10 | - - | - - | 52 | 12 | 48 |
| 4 | 10 | 1 | 2 | - - | - - | 94 | 2 | 6 |
| 5 | 10 | 2.5 | 5 | - - | - - | 61 | 10 | 39 |
| 5 | 10 | 5 | 10 | - - | - - | 10 | 39 | 90 |
| 7 | 10 | 5 | >10[b] | - - | - - | 0 | 39 | 100 |
| 8 | 18 | 5 | 10 | 2 | 1 | >13 | <50 | <87 |
| 9 | random | n/a | n/a | random | n/a | n/a | n/a | n/a |

[a] Diagrams and tests of spatial pattern analysis using these designs are shown in Figures 5 and 6.
[b] Overlapping root crowns.

ancies between actual and estimated pattern occurred for designs with very sparse or very dense vegetation cover and large differences between patch and space size (e.g. designs 2 and 7, Table 1). This confirms that correlograms tend to detect a patch size equal to one-half the total unit of pattern (patch+space), a phenomenon related to the 'drift' noted by Errington (1973). To account for this imprecision, we grouped our significant Moran's I values into three distance categories.

*Use of pseudoreplicate plots*

Plots were pseudoreplicates of the two vegetation types (Figure 1); however, the transition zone between areas with and without juniper did not coincide with any apparent or mapped environmental gradient (Driscoll, 1964). In fact, plots sampled in apparently similar, closely-spaced sites proved to have surprisingly different spatial structures, with no obvious differences in correlograms between sagebrush-grass and juniper-sagebrush-grass plots (Roberts, 1994). This was the case even though each field sampled plot was centered in the middle of a homogeneous area of bare soil and grasses. Only in hindsight could plots be selected whose correlograms illustrate the average contrasts in spatial patterns between the sagebrush-grass community and the juniper-sagebrush-grass community (Figure 5).

We filtered and combined spatial autocorrelations to compensate for between-plot variation and to account for other limits of spatial pattern detection (Roberts, 1994). We considered only those Moran's I values that were significant for a given lag in more than one soil property in a plot or more than one plot for a soil property. We grouped these Moran's I values into distance categories (0.5 – 2.8 m, 3 – 9 m, and 10 – 25 m), and combined them for all replicate plots in a community type.

## Results

The presence of juniper was associated with increased bare area and smaller, more widely spaced grass and sagebrush plants. Bare patches occupied nearly 50% of the area of juniper-sagebrush-grass plots compared to only 30% in sagebrush-grass plots (Table 2), while grass and sagebrush cover were 25 and 33% lower in the juniper-sagebrush-grass community compared to the sagebrush-grass community. Mean nearest-neighbor distances for grass, sagebrush and juniper were 0.3 – 0.4 m, 2.0 – 2.5m and 19 m; mean sizes were 0.26 – 0.35 m, 0.7 – 0.8 m and 2.9 m (Table 2, Figure 6). Grass clumps and sagebrush plants were more widely spaced and slightly smaller in the juniper-sagebrush-grass community compared to the sagebrush-grass community (Table 2, Figure 6).

Soil arthropod numbers and biomass in plots with juniper were only roughly one-fifth of those in sagebrush-grass plots (in December) (Table 3). However, mean values of other properties did not differ between community types. Soils under juniper canopies resembled (were not significantly different from)

*Table 2.* Size and spacing of grass clumps, sagebrush, and juniper in sagebrush-grass and juniper-sagebrush-grass plots. Numbers are based on mean nearest-neighbor distances

| | Sagebrush-grass | Juniper-sagebrush-grass |
|---|---|---|
| Grass clumps | | |
| *n* | 56 | 44 |
| Mean diameter (m) | 0.35 | 0.26 |
| Mean spacing (m) | 0.37 | 0.43 |
| Median spacing (m) | 0.35 | 0.35 |
| % cover | 39 | 30 |
| Sagebrush clumps | | |
| *n* | 96 | 68 |
| Mean diameter (m) | 0.8 | 0.7 |
| Mean spacing (m) | 2.0 | 2.5 |
| Median spacing (m) | 1.7 | 1.9 |
| % cover | 27 | 18 |
| Juniper trees | | |
| *n* | | 18 |
| Mean diameter (m) | | 2.9 |
| Mean spacing | | 18.7 |
| Median spacing | | 16.9 |
| % cover | | 6 |
| Bare areas | | |
| Mean diameter (m) | 0.41 | 0.46 |
| % cover | 34 | 47 |

*Table 3.* Significant differences in soil properties by season (December, May) and community type (sagebrush-grass, juniper-sagebrush-grass) based on independent (uncorrelated) samples. Moisture and initial $NO_3$–N units are for oven-dry soil weight. Means in the same column followed by the same letter are not significantly different based on ANOVA with a post-hoc Tukey's highest significant difference test with an overall $p < 0.05$

| | | Initial | | | Arthropod |
|---|---|---|---|---|---|
| | | Moisture | $NO_3$–N | VAM | biomass |
| | *n* | (%) | ($\mu$g/g) | (%) | ($\mu$g) |
| December | | | | | |
| Sagebrush-grass | 40 | 18.3a | 1.9a | 32a | 3438a |
| Juniper-sagebrush-grass | 31 | 17.1a | 2.1a | 38ab | 597b |
| May | | | | | |
| Sagebrush-grass | 60 | 2.6b | 0.7b | 39ab | 61c |
| Juniper-sagebrush-grass | 60 | 2.4b | 0.6b | 40b | 45c |

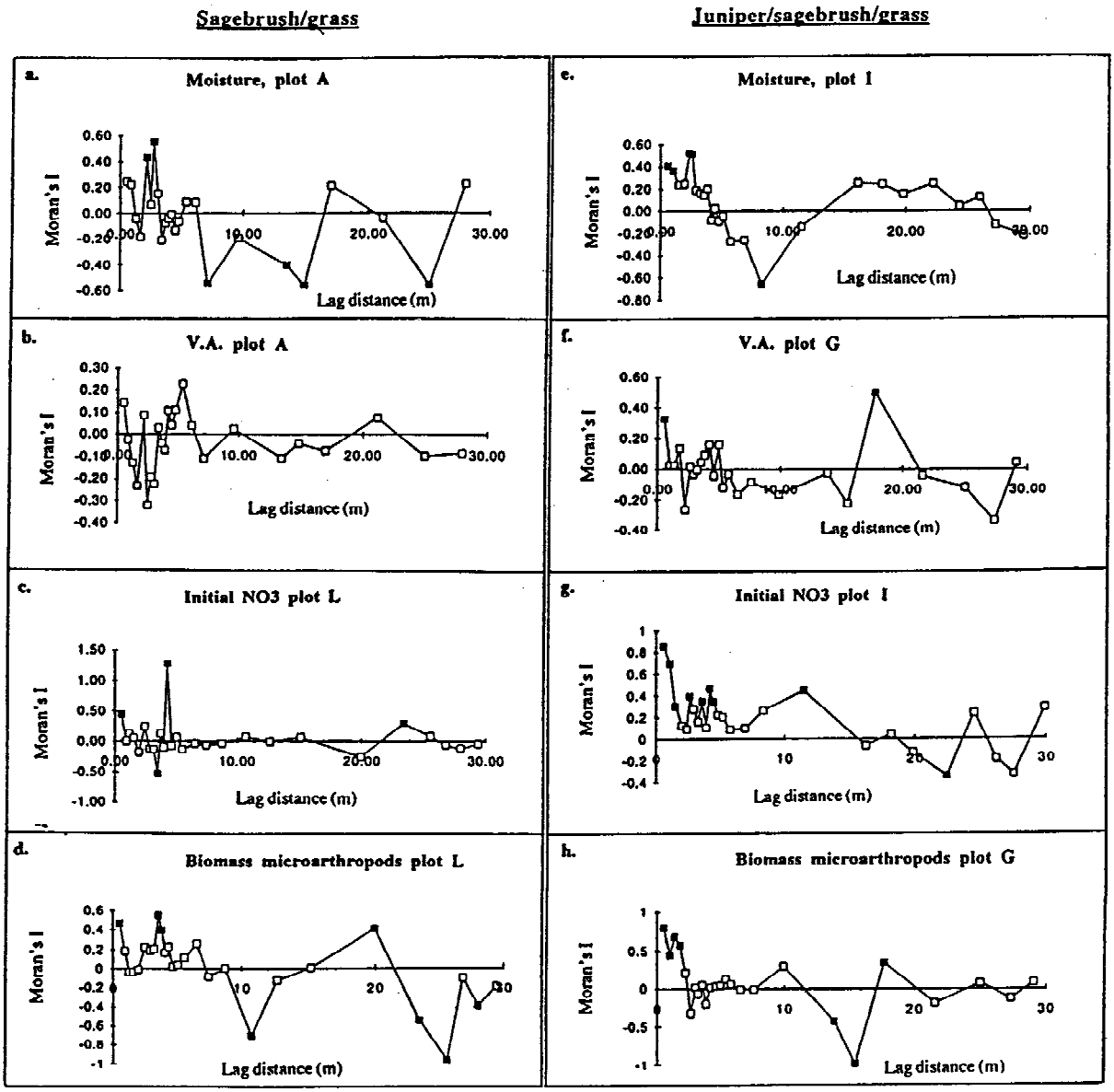


*Figure 5.* Moran's I correlograms for soil moisture, VAM, initial nitrate and soil arthropod biomass from sagebrush-grass and juniper-sagebrush-grass plots, illustrating idealized behavior of correlograms and the value of replication. Note that no single plot contained the spatial patterns displayed by groups of replicate plots, instead these correlograms were selected *post facto* to display the overall differences in spatial patterns between plots with juniper and plots without juniper, which are only apparent when all spatial autocorrelation data are combined (Figure 8). Significant values of Moran's I are more frequent at lags less than 3 m and less frequent at lags >3 m in the juniper-sagebrush-grass plots (I and G) compared to the sagebrush-grass plots (A and L).

soils of bare areas more than soils under sagebrush or grass canopies with respect to moisture content, nitrification, and net nitrogen mineralization (Table 4). However, soils under juniper canopies resembled soils under sagebrush or grass canopies with respect to arthropod numbers and biomass, and they had significantly higher VAM infection than soils under other cover types in December (Table 4). Soils in bare areas had significantly lower numbers and biomass of arthropods, fungivores, and predators compared to sagebrush and grass in both December and May (Roberts, 1994; Table 4).

Seasonal differences in soil properties exceeded differences among soils by vegetation type. The trans-

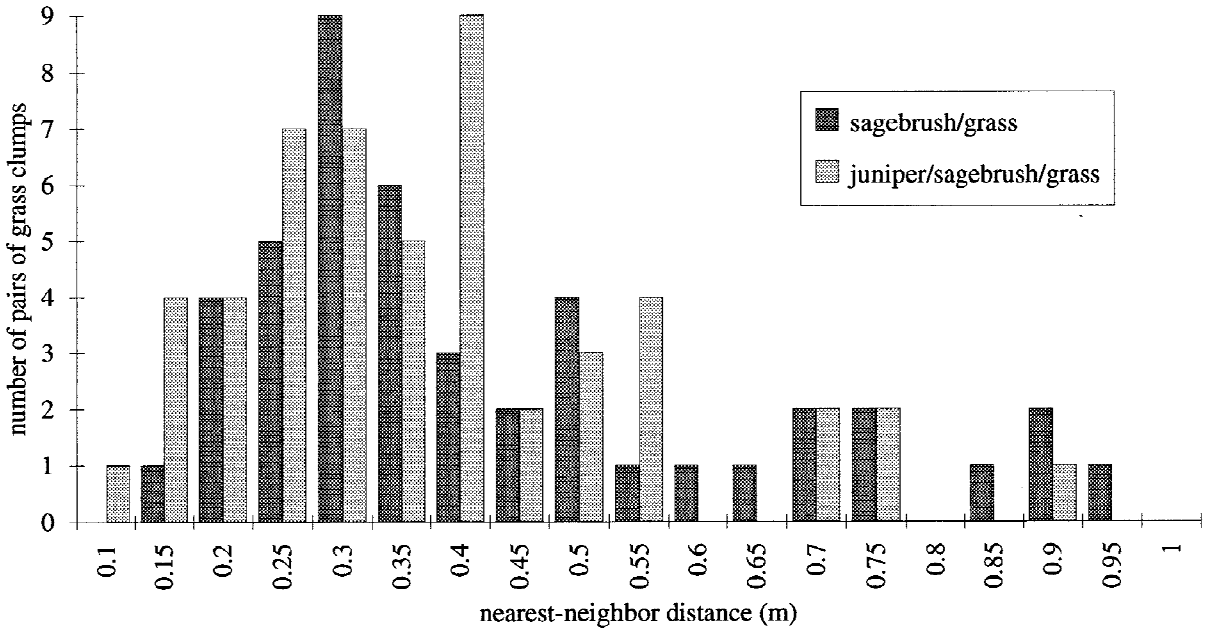


*Figure 6a.* Observed nearest-neighbour distances between grass clumps, by community type, sagebrush-grass vs. juniper-sagebrush-grass communities, in the study area.

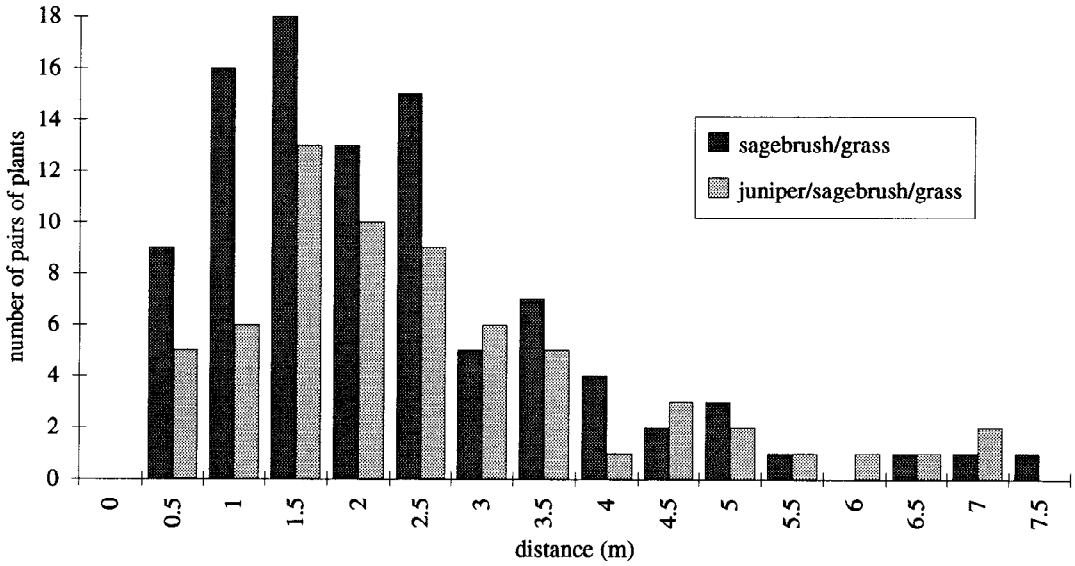


*Figure 6b.* Observed nearest-neighbour distances between sagebrush plants by community type, sagebrush-grass vs. juniper-sagebrush-grass communities, in the study area.

ition from cool wet winter conditions (December) to warm dry summer conditions (May) produced an order-of-magnitude decline in soil moisture percent and one to two orders-of-magnitude decline in soil arthropod numbers and biomass. Net nitrification and net N mineralization potential (i.e. in moistened, incubated samples) nearly doubled over this same period while VAM infection and pH did not change (Table 4). Compared to bare soils, soils under sagebrush had roughly two times higher moisture content (in May),

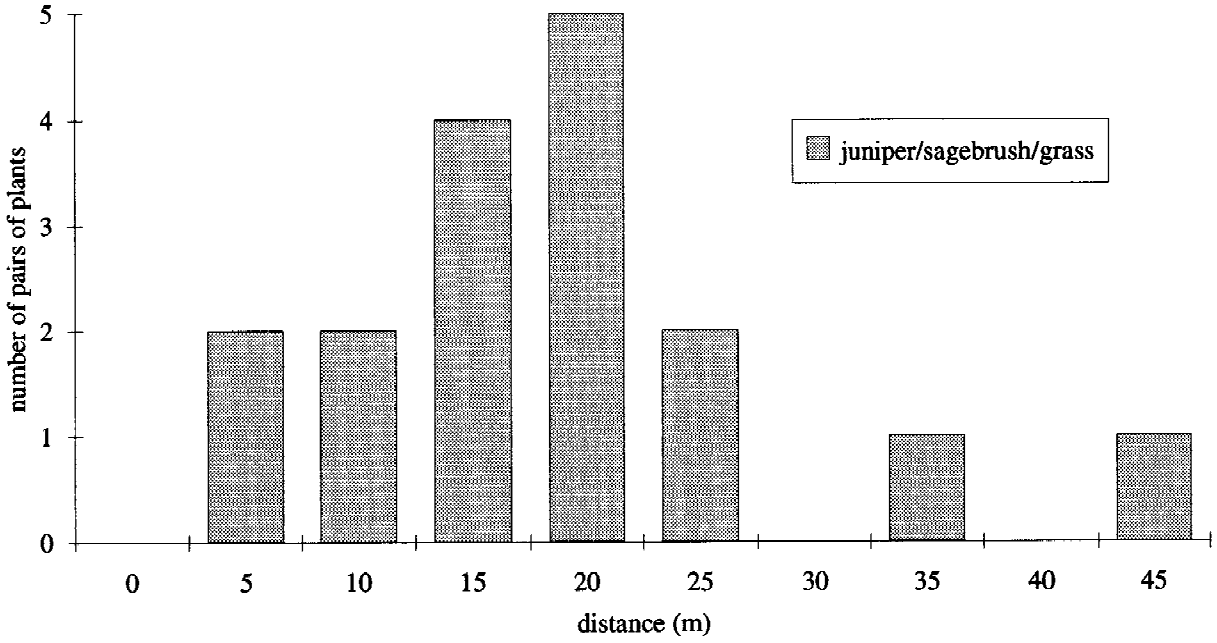


*Figure 6c.* Observed nearest-neighbour distances between juniper plants by community type, sagebrush-grass vs. juniper-sagebrush-grass communities, in the study area.

two times higher net nitrification (in December and May) and five times higher arthropod biomass (in December and May) (Table 4).

Soil properties of resource islands under sagebrush and grass varied by season. In May, soils under sagebrush had significantly higher moisture, VAM infection, $NH_4$–N, $NO_3$–N, nitrification, net N mineralization, and soil arthropods compared to bare areas, but in December, soils under sagebrush were distinguished from bare areas only by higher pH, $NO_3$–N, nitrification and soil arthropods (Table 4). In May, grasses had higher VAM, nitrification, and soil arthropods compared to bare areas, while in December grasses had higher $NO_3$–N, nitrification, and net N mineralization. Perhaps because of small sample sizes, patches under juniper were distinguished from bare areas only by higher $NH_4$–N, $NO_3$–N, and nitrification in December and by higher pH, VAM infection and soil arthropods in May (Table 4).

The dominant soil pattern in both sagebrush-grass and juniper-sagebrush-grass plots was regularly-distributed patches spanning a range of sizes and spacings. The spatial structure of most soil properties resembled regular patterns more closely than random patterns in eight of the nine plots (Figure 7). The spatial structure of VAM infection was not distinguishable from random in any plot. In the ninth plot, all soil properties but pH had a high nugget variance and a negative slope over the shorter lags up to about 5–7 m suggesting a spatial structure below the resolution of the sampling design (0.5 m).

The spatial structures revealed by this analysis ranged from 0.5m to 25m, and were most common at lags of 1 to 9 m (Figure 8). Taking all 10 soil properties in all nine plots and considering three lags (0.5 – 2.8 m, 3 – 9 m, and 10 – 25 m), there are 270 cases in which Moran's I values might be significant, of which 149, or 55%, contained one or more significant values. Over 50% of these cases containing significant Moran's I values (75 – 149) were at lags of 1 – 9 m, corresponding to the sizes and spacing of sagebrush clumps (Figure 6). Just over 22% of cases contained significant values at lags of 10 – 25 m, corresponding to the spacing between junipers, and approximately 22% were at lags of $<1$ m, corresponding to the size or spacing between grass clumps.

Spatial structure was superficially similar for the two vegetation types, but plots with juniper had greater patchiness at shorter lags ($<3$ m), and patchiness was more developed for soil moisture, net nitrification, and net N mineralization, whereas sagebrush-grass plots had greater patchiness at longer lags (3 – 9 m) and patchiness was more developed for $NO_3$–N, arthropod numbers and biomass (Figures 7 and 8). Over

*Table 4.* Mean values of soil properties by season and vegetation cover type at the sampled location in plots on the Island, central Oregon. Points in all subplots were used. Units are mg/g oven-dry soil for all properties except pH, VAM infection (% of root length), arthropods (numbers per sample) and arthropod biomass ($\mu$g per sample). Means followed by the same letter in the same row for a given season are not significantly different from one another based on ANOVA with a post-hoc Tukey's highest significant difference test with an overall $p < 0.05$

| | December | | | | May | | | |
|---|---|---|---|---|---|---|---|---|
| Soil property | bare | Grass | Sagebrush | Juniper | Bare | Grass | Sagebrush | Juniper |
| *n* | 66 | 66 | 30 | 16 | 152 | 112 | 43 | 5 |
| Moisture content | 16a | 18a | 16a | 15a | 2a | 2a | 3b | 3ab |
| pH | 6.4a | 6.3a | 6.6b | 6.8b | 6.4a | 6.3b | 6.4a | 6.4ab |
| VAM infection | 32a | 34a | 38ab | 45b | 35a | 42b | 43b | 37ab |
| $NH_4$–N | 0.3a | 0.6a | 0.4a | 0.9a | 1.3a | 2.1b | 1.7b | 2.7b |
| Ammonification | 0.2a | –0.5a | 0.0a | 0.1a | –1.7a | –2.1a | –0.7a | –1.7a |
| $NO_3$–N | 1.1a | 1.6b | 1.9b | 1.6ab | 0.5a | 0.4a | 0.7b | 0.9b |
| Nitrification | 3.8a | 8.2b | 6.2c | 3.8ac | 7.1ac | 10.2bc | 11.6b | 6.0c |
| Net N mineralization | 4.1a | 7.8b | 6.2ab | 4.4a | 6.2a | 8.2ab | 10.1b | 6.8ab |
| Soil arthropods | 23a | 58b | 89b | 66b | 1a | 3b | 4b | 3ab |
| Soil arthropod biomass | 606a | 2539b | 3647b | 2129b | 17a | 68b | 51b | 8ab |

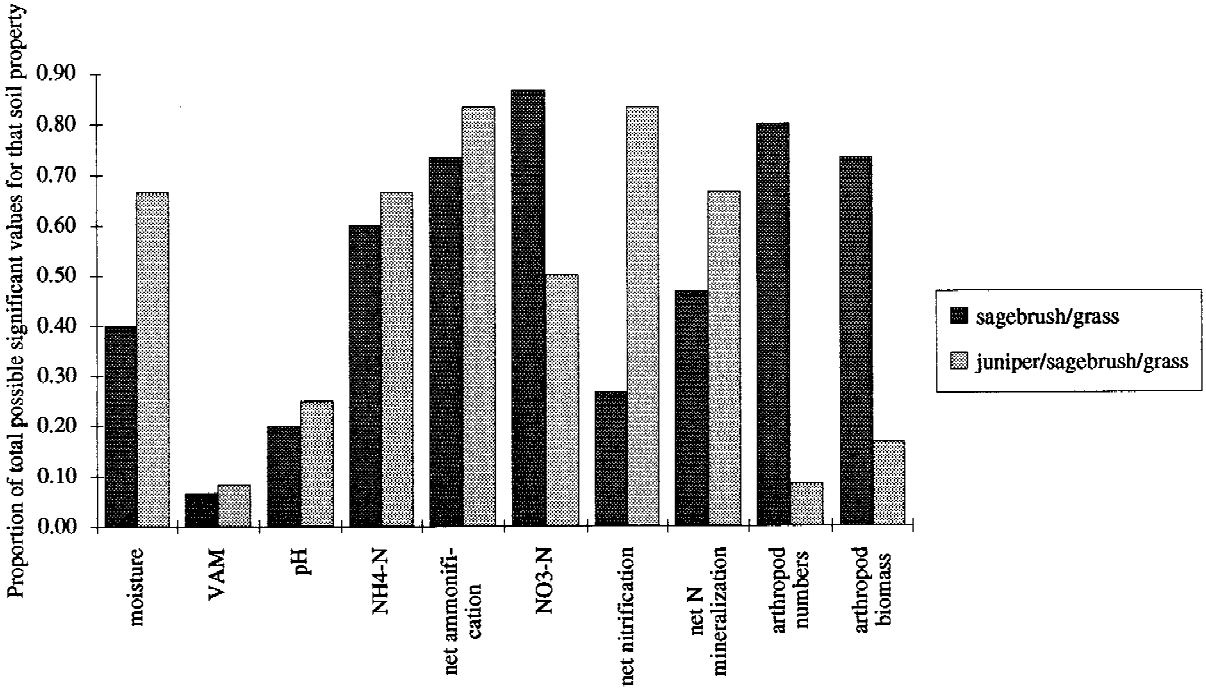


*Figure 7.* Proportions of significant values of Moran's I by soil property and vegetation type. For each soil property $n = 15$ for sagebrush-grass (three distance classes in each of 5 plots) and $n = 12$ for juniper-sagebrush-grass communities (three distance classes in each of 4 plots) for a total of 270 possible significant values. Ammonification (21 cases) and initial nitrate (19 cases) showed the greatest amount of spatial structure, followed by initial ammonium (17 cases), net N mineralization (15 cases), nitrification (14 cases), soil moisture (14 cases) and soil arthropod numbers and soil arthropod biomass (13 cases).

all lags, the number of significant Moran's I values was similar for the two vegetation types (87/150 or 58% for sagebrush-grass and 69/120 or 58% for juniper-sagebrush-grass plots) (Figure 8). However, juniper-sagebrush-grass plots showed greater spatial structure than sagebrush-grass plots at short ranges

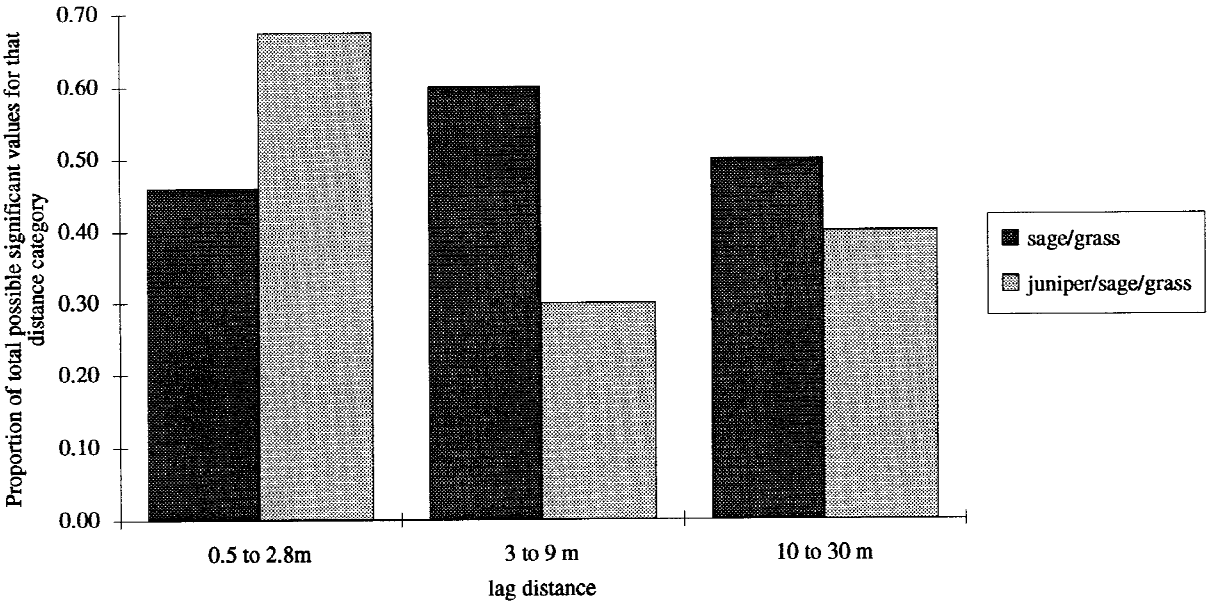


*Figure 8.* Proportions of significant values of Moran's I by distance class and vegetation type. For each distance class $n = 50$ for sagebrush-grass (ten correlograms of soil properties in each of 5 plots) and $n = 40$ for juniper-sagebrush-grass communities (10 correlograms of soil properties in each of 4 plots) for a total of 270 possible significant values. Of the possible Moran's I values at lags of 0.5 – 2.8 m, over 65% were significant in juniper-sagebrush-grass plots, but only 45% were significant in sagebrush-grass plots. Of the possible Moran's I values at lags of 3.0 – 9 m, over 60% were significant in sagebrush-grass plots, but only 30% were significant in juniper-sagebrush-grass plots.

(<3 m), while sagebrush-grass plots showed greater structure than juniper-sagebrush-grass at longer ranges (>3 m) (Figure 8). Almost half (24 of 56) of the significant Moran's I values in juniper-sagebrush-grass plots but less than a third (27 of 93) in sagebrush-grass plots occurred at lags <3 m. In contrast, 70% of significant Moran's I values in sagebrush-grass plots but only 50% in juniper-sagebrush-grass plots occurred at lags >3 m (Figure 8). The standardized semivariograms also displayed greater development of spatial structure at short ranges for juniper-sagebrush-grass communities and at long ranges for sagebrush-grass communities. The long range semivariance (lags >10 m) was greater than the short range semivariance (lags <10 m) in 30 of the 50 semivariograms for the sagebrush-grass community (60%), but only 16 of 40 semivariograms for the juniper-sagebrush-grass community (40%). Short range variation was greater than long range variation in 16/40 (40%) of cases in plots with junipers, compared to 16/50 (32%) of cases with sagebrush only (Roberts, 1994).

Over 90% of significant values of Moran's I were for moisture, N, or arthropod soil properties; pH and VA mycorrhizae rarely displayed spatial structure (Figure 7). Spatial structure in soil arthropods and initial $NO_3$–N was much more common in sagebrush-grass plots whereas spatial structure in moisture, nitrification and net N mineralization was more common in juniper-sagebrush-grass plots (see selected correlograms in Figures 5, and 7).

## Discussion

We corroborated findings of other studies showing that resource islands exist in soils under sage and grass (Charley and West, 1975, Halvorson et al., 1994, 1995, 1997; Hook et al., 1991, 1994; Jackson and Caldwell, 1993 a, b; Smith et al., 1994). Our findings also were consistent with studies that have found increased heterogeneity in soils when shrubs invade grasslands (Schlesinger et al., 1990, 1996).

However, we found previously unreported differences in pattern between replicated plots with and without juniper. These differences indicate that juniper responds to, or causes, changes in the size of resource islands under sage and grass when it invades sage-grass communities.

We found some evidence for a shift in nutrient cycling processes in the presence of juniper. Compared to soils under sagebrush or grass, soils under juniper canopies had less available nitrogen and increased VAM,

and juniper-sage-grass communities had lower arthropod biomass compared to sage-grass communities. Although moisture is inferred as a controlling factor in studies of arid grasslands (Hook et al., 1994), we found no differences in soil moisture between cover types or community types. Interestingly, soils under juniper canopies were similar to those under bare patches in their rates of nitrification and net nitrogen mineralization, but they had similar levels of arthropods as in soils under sage and grass clumps and higher levels of VAM (in December) than in soils under sage, grass or in bare areas. These findings may indicate that nitrogen mineralized by arthropods under juniper canopies is being cycled through VAM back into juniper roots. However, if juniper rooting systems are affecting moisture (Flanagan et al., 1992; Miller et al., 1987), this effect is not limited to soils under juniper canopies.

Our findings support the proposition that juniper roots explore and interact with roots of sage and grass both in bare areas and in resource islands under canopies of sage and grass. The presence of juniper was associated with increased bare area, reduction in the size and increased spacing among sage and grass plants, a reduction in arthropod biomass, increased spatial structure in soil moisture, net nitrification and net nitrogen mineralization over all lags, and increased spatial structure in all properties at short (0–3 m) lags, compared to sagebrush-grass communities. Roots were present, if not abundant, in bare areas in this study, as found in other studies of arid grasslands and sagebrush (Hook et al., 1994; Jackson and Caldwell, 1993a, b). Moreover, roots in bare areas were active, in the sense of having VAM infection and arthropod communities, albeit at lower levels than under vegetation canopies. Although juniper canopy cover was only a few percent, the rooting zone of juniper may extend into bare areas as well as into soil resource islands under sage and grass. The lower arthropod biomass and the more-developed spatial structure in moisture and nitrogen mineralization in juniper-sagebrush-grass communities is attributable to the larger bare areas and smaller sage and grass plants, rather than to changes under juniper canopies themselves. One possible explanation is that microclimatic fluctuations in communities with large bare areas cause arthropods to migrate below the shallow soil depths sampled in this study. Alternatively, this finding might imply that juniper roots are 'spatially subsidized' (*sensu* Polis et al., 1997) by resource islands under sagebrush or grass.

While our findings support the notion that juniper invasion involves the interaction of juniper roots with those of sage and grass throughout the invaded area, it is not clear whether this interaction is a cause or a result of the invasion process. The presence of invasive juniper in plots with generally larger, regularly spaced gaps supports the prediction of Bergelson et al. (1993) that weedy invaders would spread more rapidly into systems with large, regularly spaced gaps. In contrast with Schlesinger et al. (1996), who noted an increase in the size of soil resource islands following invasion by the shrub *Larrea tridentata*, we found smaller soil resource islands under sage when juniper was present. One hypothesis is that juniper invades areas which for some reason, such as shallow soils or recent fire, have relatively large regularly spaced bare patches. Microclimatic variations in bare areas might then facilitate juniper seed germination and establishment. An alternative hypothesis is that juniper invades bare patches in sage-grass communities, and then its extensive root crown is able to modify soil resource islands under clumps of sage or grass, reducing their size and density, which in turn increases the size of bare patches, thus furthering the invasion process. Since resource islands under sagebrush apparently persist for at least a decade after plots have been destroyed by fire (Halvorson et al., 1997), repeated sampling over periods of more than one decade would be required to discriminate among these hypotheses. If juniper invasion is facilitated by pre-existing large bare patches, we would expect little change in sizes of bare patches over time, whereas progressive increases in spatial heterogeneity of soil properties of juniper/sage/grass communities may indicate that juniper is facilitating its own invasion.

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