Communications

Plant–soil feedbacks and the partial recovery of soil spatial patterns on abandoned well pads in a sagebrush shrubland

Tamera J. Minnick[1,3] and Richard D. Alward[2]

[1]*Physical and Environmental Sciences, Colorado Mesa University, Grand Junction, Colorado 81501 USA*
[2]*Aridlands Natural Resource Consulting, Grand Junction, Colorado 81503 USA*

Abstract. Shrub-dominated arid and semiarid ecosystems are characterized by spatial patterns in vegetation and bare ground (e.g., resource islands). Modern oil and gas well pad construction entails complete removal of vegetation and upper soil layers, followed by replacement of soils and attempts at revegetation; historically, many pads were merely abandoned. Feedbacks between soil and vegetation are required for the recovery of ecosystem functions in these catastrophically disturbed systems. We measured soil organic carbon (SOC), employing a spatially explicit sampling protocol, on two sites in undisturbed big sagebrush communities and a chronosequence of eight recovering well pads. Sites in undisturbed communities exhibited significant spatial autocorrelation of SOC at the plot level that was absent from all of the well pad sites. Incorporating shrub presence as a covariate revealed three additional cases of SOC spatial autocorrelation on well pads. These results, along with SOC patterns between and under plants, suggest resource island development. These findings support the hypothesis that species identity as well as functional group need to be taken into account in restoration. Restoration of ecosystem functions, including those associated with resistance and resilience to disturbance, may be enhanced when characteristic soil heterogeneity and vegetation spatial patterns recover.

Key words: Artemisia tridentata; *autocorrelation; competition and facilitation; ecosystem structure and function; energy development and reclamation; plant–soil interactions; resilience; resistance; resource islands; restoration ecology; soil organic carbon; spatial analysis.*

Introduction

Disturbed ecosystems are often characterized by changes in spatial heterogeneity in both vegetation and soils (Ludwig and Tongway 1996, Tongway and Ludwig 1996). Striking consequences include increased temporal variability in productivity, lower ecosystem stability, and subsequent loss of resistance and resilience to disturbance (Herrick 2000). Ecosystem resistance and resilience, emergent properties linked to vegetation spatial patterns in arid and semiarid environments, have been described using field and modeling approaches (Breckling et al. 2005). Change in spatial structure may be a signal of a functional threshold in complex systems: e.g., loss of spatial pattern in shrubland ecosystems approaching the critical transition leading to desertification (Kefi et al.

2007) or development of significant soil spatial autocorrelation in grassland ecosystems transitioning to shrublands (Schlesinger et al. 1990).

In many arid and semiarid ecosystems, spatial patterning of vegetation and bare ground in patches or stripes can result in more efficient use of water, leading to greater plant productivity (Aguiar and Sala 1999). The development of self-organized systems have been described using Turing models (reviewed in DeAngelis 2012); such cellular automata models require feedbacks between components occurring at different spatial scales to induce self-organized vegetation patterns. Competitive interactions partially structure regular spatial patterns if roots extend beyond the plant canopy and exploit soil resources from the interspaces between plants (Barbour 1969). Rietkerk and van de Koppel (2008) have hypothesized that long-distance competition is necessary for pattern development across a variety of ecosystems. Facilitative feedbacks also play a critical role in the structure and function of ecosystems (Callaway 1995). A key facilitative feedback that can lead to
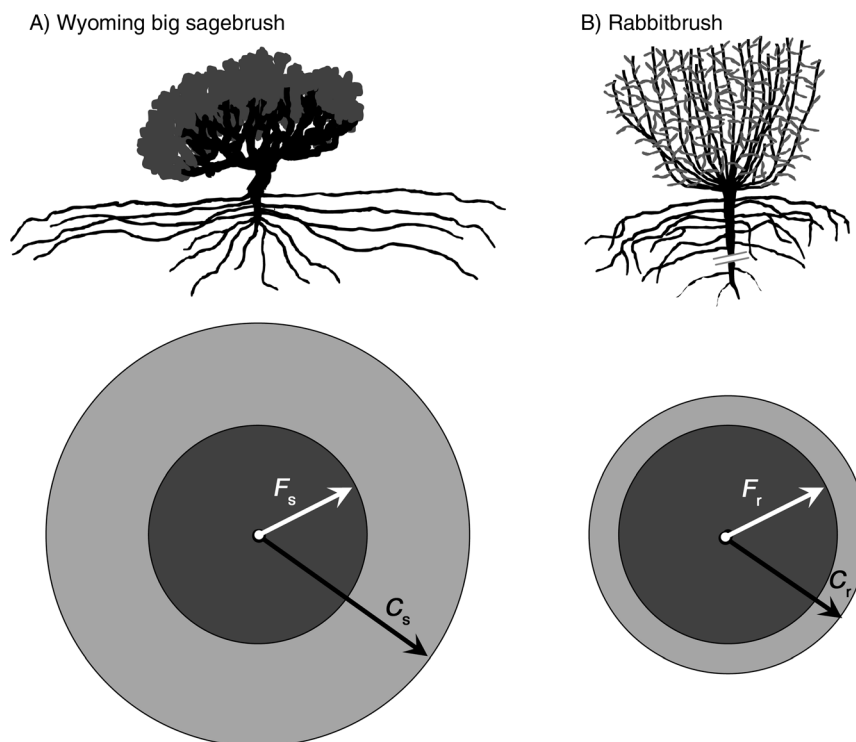
A) Wyoming big sagebrush

B) Rabbitbrush

FIG. 1.   Conceptual illustration of differences between sagebrush and rabbitbrush viewed from above and in profile (redrawn from Frischknecht 1963). Facilitation (F) is a function of canopy radius (dark circles) whereas competition (C) is a function of the lateral extent of near surface roots (light circles) (Barbier et al. 2008). Subscript s refers to sagebrush and r to rabbitbrush. (A) Big sagebrush shallow roots may extend more than twice the canopy radius. (B) In contrast, rabbitbrush has a well-developed, deep taproot and fine lateral roots that do not extend much beyond the canopy radius.

vegetative patterns on the landscape is the positive feedback between vegetation and soils resulting in the formation of resource islands (Charley and West 1975). In shrubland ecosystems, soil organic matter accumulates within the drip-line of shrubs due to the ability to trap moisture, litter, nutrients, and fine material by the canopy and because of increased decomposition of organic material under the plant (Meinders and van Breemen 2005). The facilitation : competition ratio (F:C; Fig. 1), based on the lateral extent of a plant canopy vs. roots, is valuable for explaining self-organizing spatial patterns of vegetation in arid shrubland ecosystems (Barbier et al. 2008).

The quantity and persistence of soil organic matter (SOM) is a unifying measure of soil quality (Schmidt et al. 2011). Soil OM is also the medium for plant–soil facilitative interactions in models describing vegetation spatial pattern formation (Meinders and van Breemen 2005). These enhanced soil chemical, biological, and physical properties make the local environment more conducive to plant germination, growth, and persistence, particularly in extreme environments (Ehrenfeld et al. 2005). Soil organic carbon (SOC), a proxy for SOM, is used as an indicator of ecosystem function and recovery (Bainbridge 2007).

Our overall goals were to examine the development of soil spatial patterns following ground-clearing distur-

bance in a sagebrush ecosystem and to explore potential plant-level mechanisms central in this development. Our first objective was to explicitly quantify spatial heterogeneity of SOC on undisturbed and disturbed sites. Recovery of broad-scale spatial patterns may indicate an ecosystem's return across critical thresholds and the reestablishment of emergent properties such as resistance and resilience to disturbance. Our second objective was to investigate plant–soil feedbacks by connecting spatial pattern of SOC to development of resource islands by individual plants. If SOC patterns covary with, as opposed to being independent of, plant presence, this indicates the importance of autogenic processes in the recovery of ecosystem function. Our final objective was to evaluate F:C ratios of different species and functional groups and to investigate how these complex interactions correspond with development of SOC patterns (Fig. 1).

METHODS

We identified a chronosequence of well pad sites that varied in time for recovery since the surface was reclaimed and revegetated (or merely abandoned in some cases) and were similar in pre-disturbance vegetation, soils, elevation, and management. We selected sites in Rio Blanco County, Colorado, USA (Appendix: Fig. A1, Table A1) managed by the U.S. Bureau of Land Management. Two were undisturbed reference sites, and

eight were on reclaimed or abandoned natural gas well pads. Well pad construction entails complete removal of vegetation and upper soil layers. Both vertical and horizontal homogenization of soil results from soil storage and subsequent replacement. Soil texture was generally sandy loam with one reference site a silt loam and one recovering well pad a loamy sand; pH and conductivity were somewhat elevated on recovering sites compared to reference sites, which could indicate mixing of surface and subsurface soils (Appendix: Table A1). We chose sites that had been abandoned or the well completed approximately every decade, locating seven sites from 1961, 1971, 1976, 1982, 2000, 2004, and 2008 and the two reference sites on one ridge. No appropriate sites from the late 1980s or 1990s were available on this ridge, thus the 1995 site is located one ridgeline to the south. The 2008 site had recently been recontoured and seeded. At this site, woody vegetation removed during well pad preparation was finely chopped and stored onsite; this organic matter was partially mixed into stored topsoil prior to replacement during reclamation (M. Shoemaker, *personal communication*).

Long-term data (1981–2010) from four weather stations within 60 km of our site indicate annual precipitation of 291–455 mm, annual mean maximum temperatures of 14.7–19.2°C, and annual mean minimum temperatures of −3.9°–0.1°C (Appendix: Fig. A1, Table A2). Undisturbed vegetation is a mix of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) and pinyon–juniper communities (*Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little). Other common shrubs, primarily on disturbed sites, include rubber rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom and Baird) and yellow rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.; nomenclature follows USDA PLANTS database; *available online*).[4]

At each site, we sampled a 9 × 12 m main plot, choosing a level, topographically uniform area to avoid anisotropic effects (Appendix: Fig. A2) sensu Schlesinger et al. (1996). We obtained a soil sample at each of 112 sampling points using a 5 cm diameter core to a depth of approximately 15 cm. At each point, we recorded the plant species and functional type, if present (tree, shrub, forb, perennial grass, annual grass). Sampling was completed over an 18-day period from late May to mid June, 2009. Vegetation data were collected to address questions of feedbacks on soil quality and patterns, not to characterize the vegetation communities. Soil sampling points were determined to be under a plant if any part of the plant canopy overlaid any part of the core.

Soil organic carbon (SOC) was determined using the Walkley-Black method (Nelson and Sommers 1996) after air drying and grinding samples through a 2-mm screen (Soil Grinder Model H-4199; Humboldt Manufacturing, Schiller Park, Illinois, USA). Within each site, values for SOC were transformed to meet conditions of

normality using the unbounded Johnson transformation (S_U; Slifker and Shapiro 1980). To address our first objective, we used semivariogram analyses to detect spatial autocorrelation within each site (GS[+]; Gamma Design Software, Plainwell, Michigan, USA). When spatial autocorrelation is present, two points closer together will have more similar SOC than two points further apart until the range (A_0) is reached (Goovaerts 1998). To address our second objective of determining if spatial autocorrelation of SOC covaried with plant presence, we performed cross-variogram analyses for each site using as a covariate indicator the presence or absence of shrub cover or perennial grass cover. In this analysis, spatial autocorrelation is determined using only points of contrasting cover classes (Goovaerts 1998). We fit semi- and cross-variograms to a spherical model where lack of fit indicates lack of spatial autocorrelation (Schlesinger et al. 1996). We used kriging to estimate SOC between the sampled points to map the patterns described by the simple semivariogram analysis. Kriging was performed on untransformed data for ease of interpretation.

To further address our second objective, we recalculated Johnson S_U transformations of SOC for all samples across all sites and performed a split-plot ANOVA using JMP 9.0 (SAS Institute 2009). Site was a random-effect whole-plot factor. The fixed-effect subplot factor, nested within site, was presence or absence of plant cover divided into three categories: (1) under a shrub canopy, (2) under a perennial grass canopy, or (3) the interspaces between plants. We used planned contrasts to compare SOC means within each site.

RESULTS

There are striking differences in spatial patterns of SOC among undisturbed and disturbed sites as depicted in the kriged maps (Fig. 2A and B, column i vs. Fig. 2C–J, column i). Soil OC exhibits spatial autocorrelation within undisturbed reference soils in this shrub ecosystem (Fig. 2A and B, column ii; Appendix: Table A3). The site abandoned in 1982 was typical of the younger disturbed sites (excluding the 2004 site) in that it exhibited spatial autocorrelation in SOC, but the value for the range was large ($A_0 > 6.0$ m). This indicates spatial autocorrelation on a scale greater than that of the typical plant size (Fig. 2F–H and J, column ii; Appendix: Table A3). The 1961 and 1971 disturbed sites exhibited no spatial autocorrelation (Fig. 2C and D, column ii; Appendix: Table A3). Sites abandoned in 1976 and 2004 exhibited spatial autocorrelation (Fig. 2E and I, column ii; Appendix: Table A3). However, for both, the nugget variance was high relative to sill variance. Thus, a low proportion of variation was accounted for in the model, indicating that much of the spatial autocorrelation was at a scale smaller than sampled. This may indicate heterogeneity induced by rocks or the introduced annual grass, *Bromus tectorum*, the species most frequently associated with sampling points on this well pad (Table 1).

Cross-variogram analyses, incorporating shrub presence or absence as a covariate, revealed additional cases of spatial autocorrelation in SOC, but adding perennial
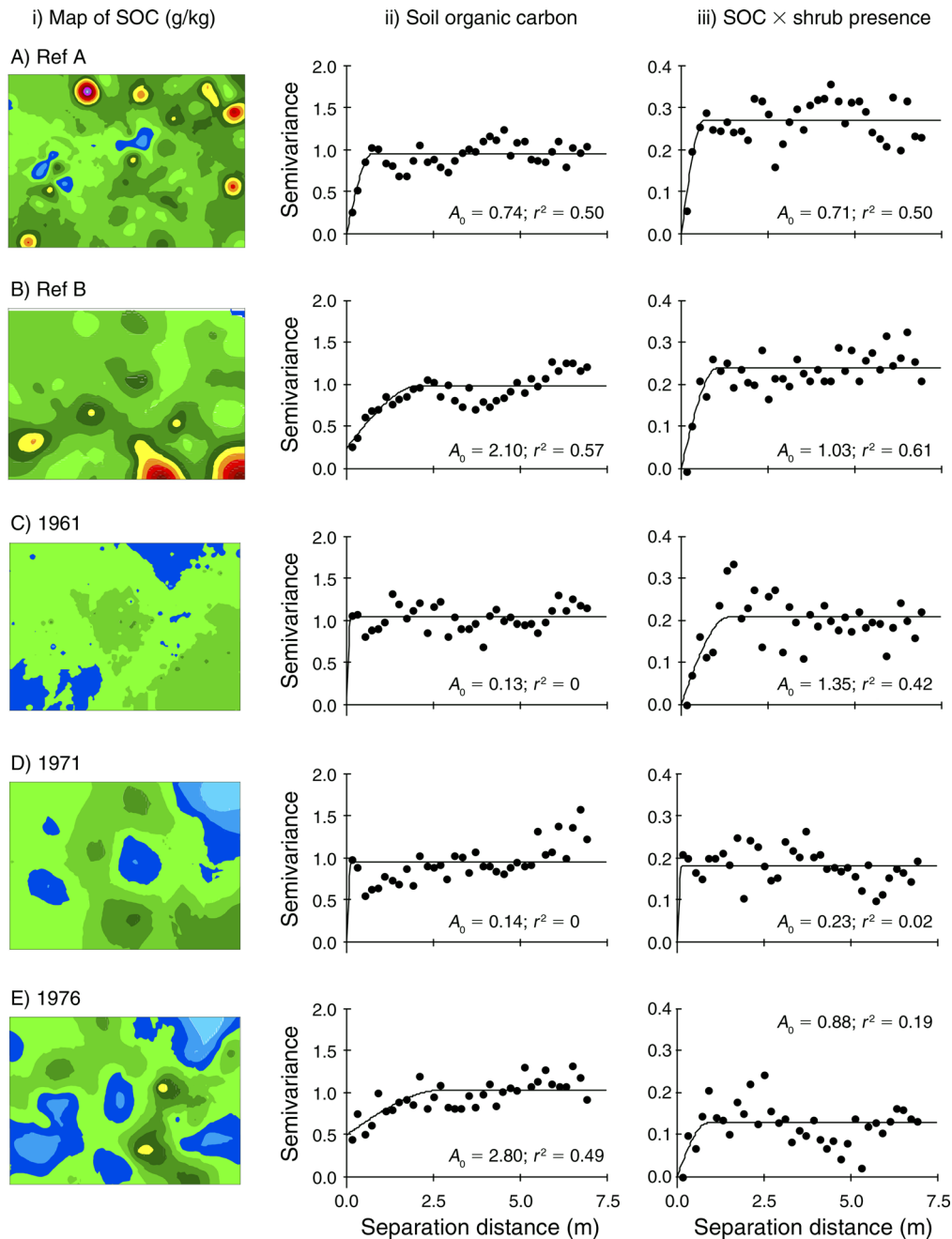
FIG. 2. Spatial patterns in soil organic carbon (SOC) for (rows A–B) two reference sites, and (rows C–J) a chronosequence of abandoned or reclaimed well pads. Each site is described with a triplet of panels. (i) A kriged map depicting SOC interpolated from 112 soil samples; SOC varies in 2 g C/kg soil increments from 4 (pale blue) to 34 (pink) g C/kg soil. (ii) Spherical model semivariogram for the distribution of SOC; each point represents the mean semivariance for all pairs of samples within each 0.2-m interval of separation distances between 0.2 and 7.0 m. (iii) Cross-covariate semivariogram for the distribution of SOC with the presence or absence of a shrub canopy over each sampling point as the covariate (except for (J) 2008, which had no vegetation). A_0 is the range or the distance at which the two point values are no longer correlated. The r^2 for the relationship indicates the proportion of variance explained by spatial autocorrelation.

grass presence or absence as a covariate did not (Appendix: Table A4). Four sites exhibited spatial autocorrelation with the shrub covariate (Fig. 2A–C and F, column iii; Appendix: Table A4). For three of these sites (Ref A, Ref B, 1961), nearly every soil sample

was located beneath big sagebrush among the samples that were under a shrub canopy (Table 1). The fourth site (1982) exhibited spatial autocorrelation with a shrub covariate, despite none of the soil samples being located beneath sagebrush (Fig. 2F, column iii; Table 1; and

i) Map of SOC (g/kg)   ii) Soil organic carbon   iii) SOC × shrub presence

F) 1982

$A_0 = 1.62; r^2 = 0.36$

$A_0 > 7.0; r^2 = 0.79$

G) 1995

$A_0 = 1.42; r^2 = 0.13$

$A_0 = 6.64; r^2 = 0.75$

H) 2000

$A_0 = 0.33; r^2 = 0.07$

$A_0 > 7.0; r^2 = 0.72$

I) 2004

$A_0 = 0.32; r^2 = 0.001$

$A_0 = 0.86; r^2 = 0.47$

Separation distance (m)

J) 2008

$A_0 = 6.16; r^2 = 0.78$
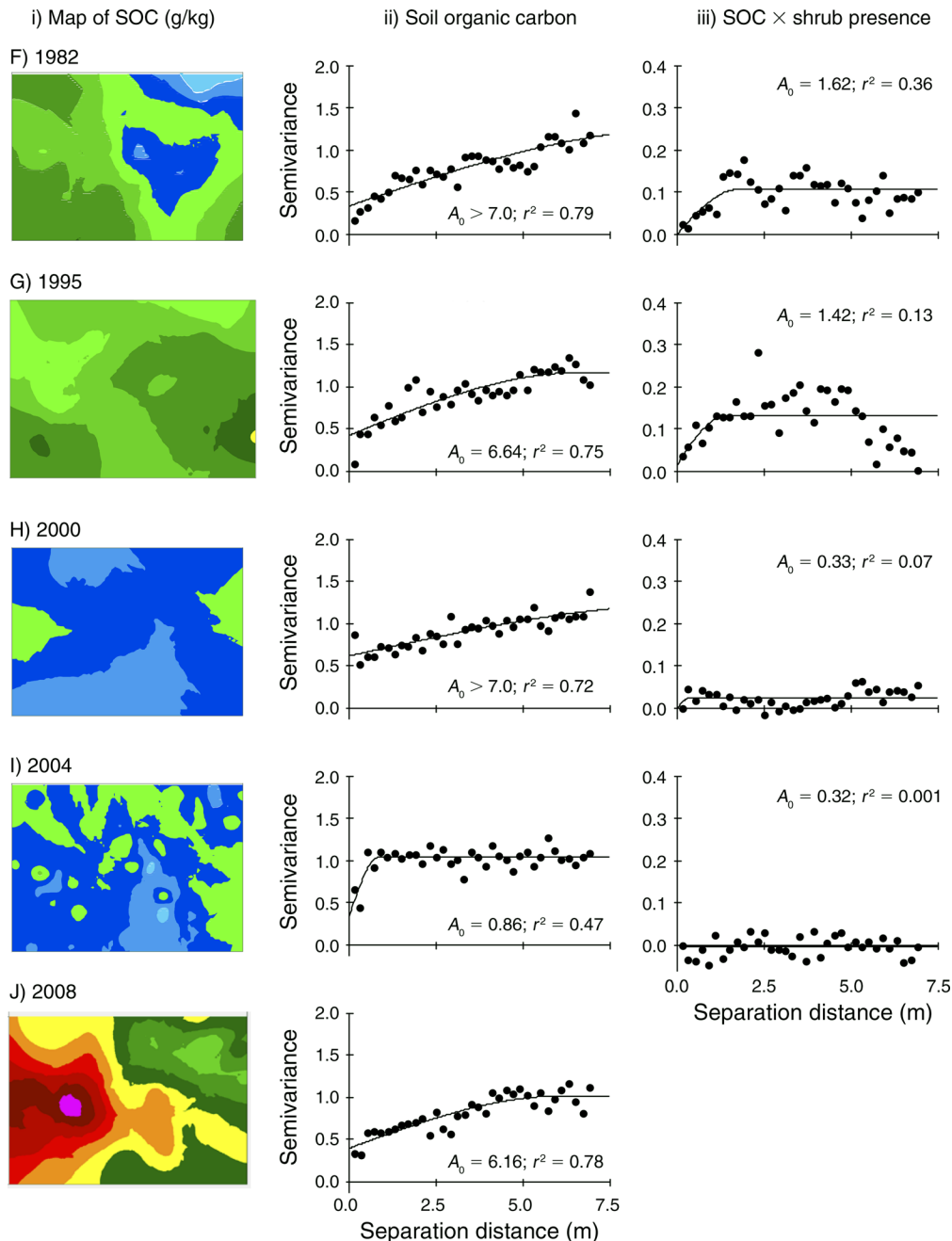
Separation distance (m)

FIG. 2. Continued.

Appendix: Table A4). This low frequency of sagebrush is a characteristic the 1982 site has in common with the remaining sites that initiated recovery since 1961. On the sites 1971–2004, fewer than half of the soil samples located beneath shrub cover were under sagebrush; 65–99% of the samples beneath shrubs were under rabbitbrush. The 1982 site, along with the other sites exhibiting spatial autocorrelation, has a higher perennial grass:shrub ratio with a large proportion of those perennial grasses located in the interspaces between shrub canopies (Table 1). The 1976 and 1995 site results are consistent with the development of spatial autocorrelation, but the model r^2 was very low (Fig. 2E and G, column iii; Appendix: Table A4). The 1971, 2000, and 2004 sites lacked spatial autocorrelation (Fig. 2D, H, and I, column iii; Appendix: Table A4).

Mean SOC of samples obtained beneath perennial plant canopies was significantly higher than in the interspaces on the reference sites and well pads completed prior to 1995 (Fig. 3). For these sites, mean SOC under

Communications

shrub canopies (9.6–14.1 g C/kg soil for recovering sites; 16.6–17.0 g C/kg soil for reference sites) was always significantly higher than in the interspaces (8.5–12.8 g C/kg soil); however, only in the cases of the 1976 and 1982 sites was SOC under perennial grass canopies significantly higher than those in the interspaces. Mean SOC did not differ significantly under perennial plants compared to the interspaces for the well pad sites abandoned in 1995, 2000, 2004, and 2008; in all of these cases either perennial grasses or perennial shrubs or both were absent or scarce (Table 1). High SOC on the 2008 site likely reflects the presence of finely chopped slash redistributed with topsoil during reclamation.

DISCUSSION

In big sagebrush ecosystems, SOC typically exhibits strong autocorrelation distances (the range or A_0; Fig. 2, Appendix: Table A3) that correspond to the dimensions of the dominant vegetation and interspaces (Halvorson et al. 1994). None of the abandoned well pads exhibit both SOC concentration and spatial patterning at the plot-level characteristic of the reference sites, despite having up to 47 years for recovery (Fig. 2A–J, column ii; Appendix: Table A3). This is longer than the 32 years for recovery McGonigle et al. (2005) predicted from an eight-year study of SOC accumulation under *A. tridentata* spp. *wyomingensis* growing on subsoil fill material. It follows that important ecosystem properties and functions likely have not recovered. For instance, soil heterogeneity in shrublands may increase diversity and productivity (Aguiar and Sala 1999). Spatial patterning of soil resources may resist disturbance and confer ecosystem resilience. In North American sagebrush steppe, fire is a well-studied disturbance in which it has been documented that SOC patterns persist postfire (Sankey et al. 2012) and native seedling germination following fire was more likely where sagebrush had been present than in interspaces (Boyd and Davies 2010).

Slow recovery following catastrophic disturbance associated with well pad construction may be due to exceedance of both biotic and abiotic thresholds of degradation (sensu Whisenant 1999). In this two-threshold model, compromised primary processes of the physical environment need repair to allow feedbacks with reestablishing vegetation to drive recovery of ecosystem processes through autogenic means (Whisenant 1999). This conceptual partitioning of abiotic and biotic constraints can also inform the restoration of these degraded systems (King and Hobbs 2006). In less severely damaged systems, where neither abiotic nor biotic thresholds have been crossed, recovery may be initiated by removing drivers of degradation (Bestelmeyer et al. 2013).

Although 47 years was insufficient time for recovery of plot-level patterns of SOC, we did detect evidence for plant–soil feedbacks at the individual plant scale identified in our second objective. Well pads that had 26 or more years for recovery (i.e., 1961–1982) exhibited higher SOC concentrations under vs. between shrubs (Fig. 3). Additionally, development of spatial autocorrelation

from the presence of these resource islands was evident from the results of cross-covariogram analyses; some of the older well pads exhibited SOC spatial autocorrelation when shrub location was taken into account (Fig. 2C–G, column iii; Appendix: Table A4). In contrast, cross-variograms that incorporated perennial bunchgrass presence failed to identify significant spatial autocorrelation in SOC (Appendix: Table A4). These results are similar to those of Schlesinger et al. (1996) who detected spatial autocorrelation patterns in shrubland ecosystems but not in grassland ecosystems; they attributed these results to potential spatial pattern in grasslands existing on a scale finer than their sampling protocol. Lane and BassiriRad (2005) found spatial autocorrelation in restored grasslands when sampling at a finer resolution. Results from the shrub cross-variograms support Whisenant's (1999) recommendations for directing vegetation change in disturbed ecosystems to initiate and promote positive feedbacks between plants and soil.

The effectiveness of this model for repair of ecosystem function, driven by feedbacks between plants and soils, may also depend upon species and functional type identity. Differences in $F{:}C$ ratios of dominant shrub species on reference sites and recovering well pads are consistent with observed differences in development of SOC patterns. Spatial autocorrelation at the plot-level on the two reference sites may be explained by high frequency of sagebrush (Table 1): big sagebrush have a pronounced shallow lateral root system that extends well beyond the horizontal extent of the canopy, resulting in a low $F{:}C$ ratio (Fig. 1A), and big sagebrush accumulates SOC under its canopy (Halvorson et al. 1994). The emergence of resource islands on the 1961 site when shrub presence is accounted for further supports this hypothesis. Rabbitbrush, on the other hand, has a deep tap root and limited shallow roots, which result in a higher $F{:}C$ ratio (Fig. 1B; Klepper et al. 1985), and thus is not predicted to promote spatial autocorrelation. Similarly, Charley and West (1975) found plant-induced soil patterns to be much more prominent in areas dominated by big sagebrush than four wing saltbush (*Atriplex confertifolia*). The emergence of resource islands on the 1976 and 1982 sites, both dominated by rabbitbrush, but not the 1971 site, challenges this hypothesis. Barbier et al. (2008) proposed that abundant grass cover may effect an apparent decrease in the shrub $F{:}C$ ratio beyond what would be expected from shrubs alone. Bunchgrasses, which have shallow, fibrous root systems, harvest resources predominantly from upper soil layers (Schenk and Jackson 2002) and may lower $F{:}C$ ratios by reducing the resources shrubs harvest from interspaces and sequester in soils beneath their own canopies.

If resistance and resilience are emergent properties of ecosystems conferred by spatial patterns, our results suggest that this sagebrush study system may require 50 years or more to recover these properties following catastrophic disturbance: we found plot-level patterns only in our two reference sites (Fig. 2; Appendix: Table A3). These plot-level spatial patterns develop from individual-scale, plant–soil feedback phenomena. Evi-

TABLE 1.   Percentage of soil samples located below vegetation canopies, separated into functional groups and three shrub species.

			Soil samples located beneath trees or shrubs (%)			Soil samples located beneath only herbaceous vegetation (%)†				Ratios‡	
Site name§	Trees	All Shrubs	*Artemisia tridentata*	*Ericameria nauseosa*	*Chrysothamnus viscidiflorus*	Perennial grass¶	Perennial forb	Annual grass#	Annual forb	Perennial grass : shrub	Perennial grass, U:B shrubs
Ref A	1	34	34	0	0	24	0	0	0	0.71	0.45
Ref B	1	30	28	2	0	54	0	0	0	1.80	0.16
1961	0	29	28	1	0	15	0	0	0	0.52	0.31
1971	0	62	20	41	0	10	0	0	0	0.16	0.43
1976	0	33	1	23	7	18	0	0	0	0.55	0.40
1982	3	19	0	13	0	15	8	0	0	0.79	0.16
1995	0	55	21	16	19	0	1	0	0	0	4.00
2000	0	4	0	0	0	39	0	7	1	9.75	0
2004	0	5	0	1	0	0	0	89	0	0	0

Note: Ref stands for reference sites.

† If a soil sample was located beneath the canopies of herbaceous vegetation and a shrub, it was counted as being beneath a shrub.

‡ Ratios are of soil samples located under perennial grasses vs. shrubs, or of samples located beneath a perennial grass canopy that were also under shrubs (U) vs. beneath only herbaceous vegetation (B).

§ The well pad site from 2008 was omitted since it was bare of vegetation.

¶ Abundant perennial bunchgrasses included *Achnatherum hymenoides*, *Bouteloua gracilis*, *Elymus trachycaulus*, and *Hesperostipa comata* (R. D. Alward, *unpublished data*).

The only annual grass species observed with the soil samples was cheatgrass (*Bromus tectorum*).

dence of individual-scale driven patterns include SOC accumulations under shrub, and sometimes grass, canopies (Fig. 3) and when shrubs were included as a covariate in the cross-covariogram analyses (Table A4). These results were seen in the 1982 and older sites, indicating that resource islands may develop and be detectable within 25 years. Similarly, prairie restoration required more than 26 years to recover characteristic soil patterns; Lane and BassiriRad (2005) found resource

island patterns in soil carbon and nitrogen at the scale of the dominant plants, in this case native C_4 grasses, accompanied by increased homogeneity at the macro scale. Resource islands have been studied across diverse ecosystems, and functional group and species identity are important for their development. Successful restoration of critical ecosystem functions may require recovery of plant–soil feedbacks in addition to reestablishing vegetation structure (King and Hobbs 2006).
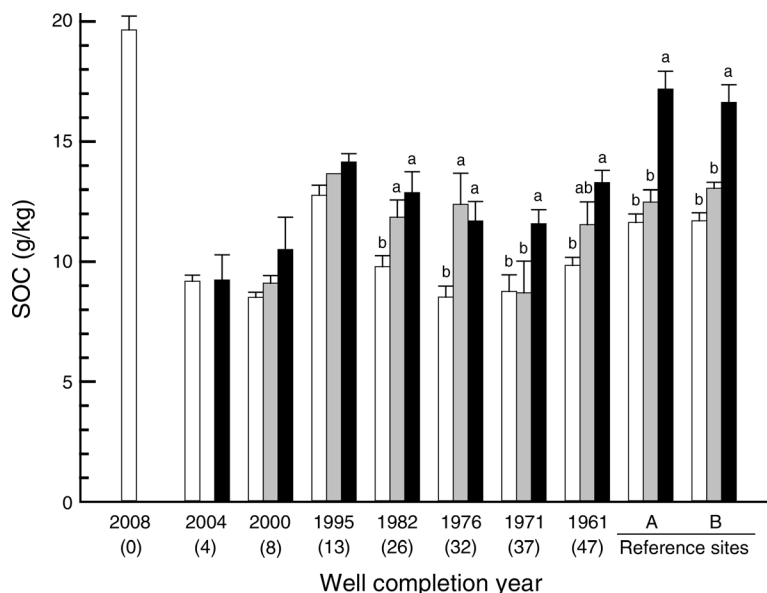

FIG. 3.   Mean soil organic carbon (+SE) for soils between perennial plants (white) or under the canopy of perennial grasses (gray) or shrubs (black) on reclaimed well pads and reference sites. A split-plot ANOVA revealed significant differences in SOC due to differences in plant canopy ($F_{17,1079} = 9.45$, $P < 0.0001$). Different lowercase letters above bars indicate significant differences ($P < 0.05$) in SOC within a site using planned contrasts. Untransformed data were plotted for ease of interpretation. Numbers in parentheses on the x-axis are the number of years for recovery.

Communications

Communications

LITERATURE CITED

Aguiar, M. R., and O. E. Sala. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution 14:273–277.

Bainbridge, D. A. 2007. A guide for desert and dryland restoration. Island Press, Washington, D.C., USA.

Barbier, N., P. Couteron, R. Lefever, V. Deblauwe, and O. Lejeune. 2008. Spatial decoupling of facilitation and competition at the origin of gapped vegetation patterns. Ecology 89:1521–1531.

Barbour, M. G. 1969. Age and space distribution of the desert shrub *Larrea divarticata*. Ecology 50:679–685.

Bestelmeyer, B. T., M. C. Duniway, D. K. James, L. M. Burkett, and K. M. Havstad. 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. Ecology Letters 16:339–345.

Boyd, C. S., and K. W. Davies. 2010. Shrub microsite influences post-fire perennial grass establishment. Rangeland Ecology and Management 63:248–252.

Breckling, B., F. Muller, H. Reuter, F. Holker, and O. Franzle. 2005. Emergent properties in individual-based ecological models—introducing case studies in an ecosystem research context. Ecological Modelling 186:376–388.

Callaway, R. M. 1995. Positive interactions among plants. Botanical Review 61:306–348.

Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. Journal of Ecology 63:945–963.

DeAngelis, D. L. 2012. Self-organizing processes in landscape pattern and resilience: a review. ISRN Ecology 2012. http://dx.doi.org/10.5402/2012/274510

Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant–soil system. Annual Review of Environment and Resources 30:75–115.

Frischknecht, N. C. 1963. Contrasting effects of big sagebrush and rubber rabbitbrush on production of crested wheatgrass. Journal of Range Management 16:70–74.

Goovaerts, P. 1998. Geostatistical tools for characterizing the spatial variability of microbiological and physico-chemical soil properties. Biology and Fertility of Soils 27:315–334.

Halvorson, J. J., H. Bolton, Jr., J. L. Smith, and R. E. Rossi. 1994. Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. Great Basin Naturalist 54:313–328.

Herrick, J. E. 2000. Soil quality: an indicator of sustainable land management? Applied Soil Ecology 15:75–83.

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

King, E. G., and R. J. Hobbs. 2006. Identifying linkages among conceptual models of ecosystem degradation and restoration: Towards an integrative framework. Restoration Ecology 14:369–378.

Klepper, E. L., K. A. Gano, and L. L. Cadwell. 1985. Rooting depth and distributions of deep-rooted plants in the 200 Area Control Zone of the Hanford Site (No. PNL-5247) Pacific Northwest National Laboratory, Richland, Washington, USA.

Lane, D. R., and H. BassiriRad. 2005. Diminishing spatial heterogeneity in soil organic matter across a prairie restoration chronosequence. Restoration Ecology 13:403–412.

Ludwig, J. A., and D. J. Tongway. 1996. Rehabilitation of semiarid landscapes in Australia. II. Restoring vegetation patches. Restoration Ecology 4:398–406.

McGonigle, T. P., M. L. Chambers, and G. J. White. 2005. Enrichment over time of organic carbon and available phosphorus in semiarid soil. Soil Science Society of America Journal 69:1617–1626.

Meinders, M., and N. van Breemen. 2005. Formation of soil-vegetation patterns. Pages 207–227 *in* G. M. Lovett, M. G. Turner, C. G. Jones, and K. C. Weathers, editors. Ecosystem function in heterogeneous landscapes. Springer, New York, New York, USA.

Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter. Pages 961–1010 *in* D. L. Sparks, editor. Methods of soil analysis, part 3, chemical methods. Soil Science Society of America Book Series 5. American Society of Agronomy, Madison, Wisconsin, USA.

Rietkerk, M., and J. van de Koppel. 2008. Regular pattern formation in real ecosystems. Trends in Ecology and Evolution 23:169–175.

Sankey, J. B., M. J. Germino, T. T. Sankey, and A. N. Hoover. 2012. Fire effects on the spatial patterning of soil properties in sagebrush steppe, USA: a meta-analysis. International Journal of Wildland Fire 21:545–556.

SAS Institute. 2009. JMP 9 modeling and multivariate methods. SAS Institute, Cary, North Carolina, USA.

Schenk, H. J., and R. B. Jackson. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology 90:480–494.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–374.

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

Schmidt, M. W. I., et al. 2011. Persistence of soil organic matter as an ecosystem property. Nature 478:49–56.

Slifker, J. F., and S. S. Shapiro. 1980. The Johnson System: selection and parameter estimation. Technometrics 22:239–246.

Tongway, D. J., and J. A. Ludwig. 1996. Rehabilitation of semiarid landscapes in Australia. I. Restoring productive soil patches. Restoration Ecology 4:388–397.

Whisenant, S. G. 1999. Repairing damaged wildlands: a process-orientated, landscape-scale approach. Cambridge University Press, Cambridge, UK.

SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/13-1698.1.sm