SPECIAL FEATURE

Multiscale responses of soil stability and invasive plants to removal of non-native grazers from an arid conservation reserve

Erik A. Beever[1]*, Manuela Huso[2] and David A. Pyke[1]

[1]*USGS Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon 97331, USA, and* [2]*Oregon State University, Department of Forest Science, Corvallis, Oregon 97331, USA*

ABSTRACT

Disturbances and ecosystem recovery from disturbance both involve numerous processes that operate on multiple spatial and temporal scales. Few studies have investigated how gradients of disturbance intensity and ecosystem responses are distributed across multiple spatial resolutions and also how this relationship changes through time during recovery. We investigated how cover of non-native species and soil-aggregate stability (a measure of vulnerability to erosion by water) in surface and subsurface soils varied spatially during grazing by burros and cattle and whether patterns in these variables changed after grazer removal from Mojave National Preserve, California, USA. We compared distance from water and number of ungulate defecations — metrics of longer-term and recent grazing intensity, respectively, — as predictors of our response variables. We used information-theoretic analyses to compare hierarchical linear models that accounted for important covariates and allowed for interannual variation in the disturbance–response relationship at local and landscape scales. Soil stability was greater under perennial vegetation than in bare interspaces, and surface soil stability decreased with increasing numbers of ungulate defecations. Stability of surface samples was more affected by time since removal of grazers than was stability of subsurface samples, and subsurface soil stability in bare spaces was not related to grazing intensity, time since removal, or any of our other predictors. In the high rainfall year (2003) after cattle had been removed for 1–2 years, cover of all non-native plants averaged nine times higher than in the low-rainfall year (2002). Given the heterogeneity in distribution of large-herbivore impacts that we observed at several resolutions, hierarchical analyses provided a more complete understanding of the spatial and temporal complexities of disturbance and recovery processes in arid ecosystems.

Keywords

Biological invasions, California, herbivory, hierarchical linear models, information-theoretic analyses, soil-aggregate stability, non-native plants, Mojave Desert, *Schismus barbatus.*

*Correspondence: Erik A. Beever, NPS Great Lakes Network, 2800 Lake Shore Dr. E., Ashland, WI 54806, USA. Tel.: 715-682-0631 xt31; Fax: 715-682-6190; E-mail: erik_beever@nps.gov

INTRODUCTION

Disturbances act on a variety of temporal and spatial scales, and they affect ecosystem components through a diversity of physical and chemical processes. In the case of ungulates, for example, spatial extent of disturbances ranges from individual wallows (usually < 10 m in diameter), to migration routes that are hundreds of kilometres long and up to several kilometres wide. In addition to this variability in extent, ungulates also exhibit heterogeneity in their patterns of consumption and movement at several spatial grains (resolutions): within-plant (different heights, floral parts vs. new or mature leaves), use of vegetated vs.

bare areas, forage preferences among plant species, use of various plant communities, and seasonal migrations (Augustine & Frank, 2001; Semmartin & Oesterheld, 2001; Kie *et al.*, 2002; Teague *et al.*, 2004). Furthermore, effects of disturbance processes are nested within landscape patterns of climate, vegetation, and soils (Archer & Smeins, 1991).

While technological advances in remote sensing, GIS, computer processing speed and spatially explicit statistical models hold promise for broadening analyses of ecological phenomena at large spatial scales, logistical, financial, and research-design constraints often restrict analyses of both disturbance and ecosystem recovery from disturbance to investigations that are both spatially and
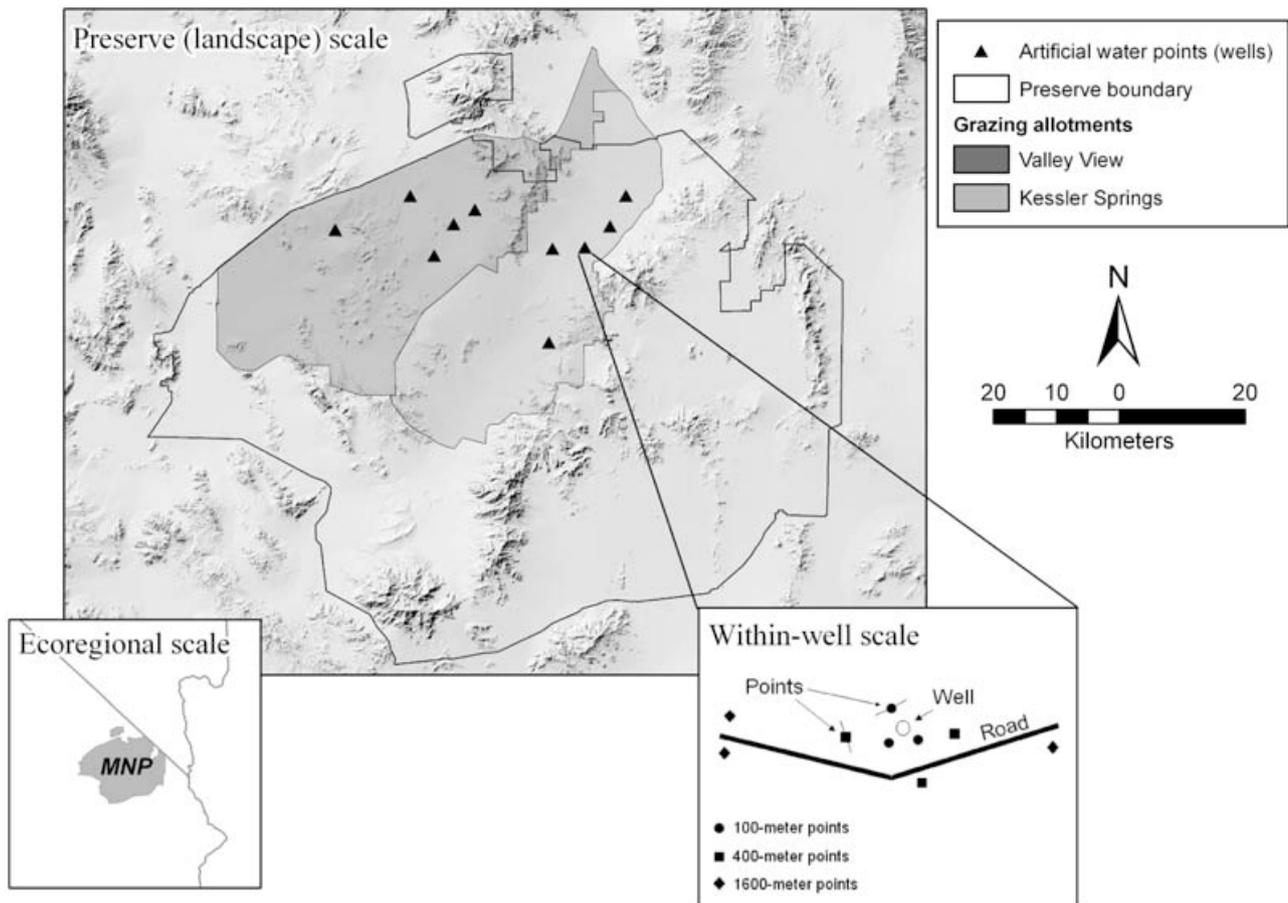
Figure 1 Depiction of our multiscale sampling strategy. Location of Mojave National Preserve within the south-western USA ('Ecoregional scale'), our study allotments and wells within MNP ('preserve scale'), and sampling locations within each well ('within-well scale'). As described in the text, we sampled at two transects per point (as shown at the two labelled points), three points at each distance from the well, and three distances.

temporally limited (May, 1994). Consequently, our fragmentary understanding of disturbance and the importance that scale and pattern of disturbance may have on ecosystem components (Kallimanis *et al.*, 2005) constitutes a challenge for conservation. For example, disturbance may cause alterations within systems that are difficult to reverse (Laycock, 1991; Rietkerk & van de Koppel, 1997). Thus, across space and time, ecosystem recovery is protracted and uncertain and may be difficult to detect.

We examined the consequences of disturbance in Mojave National Preserve (Fig. 1). Our objectives were to test whether: (1) grazing-related spatial gradients of vegetation and soil characteristics exist when grazing by cattle and feral burros occurs, (2) these grazing-intensity gradients are altered with increasing time since grazer removal, and (3) whether the dynamics of our response variables were best described only when both local and landscape variables were considered, compared to models with variables from only one scale. Because plant-community succession and ecosystem recovery can be protracted in arid systems such as the Mojave Desert, we tested these questions using variants of two response variables: soil-aggregate stability and cover of non-native annual plants. We hypothesized that they would both respond rapidly to grazing removal yet would vary in the

spatial grain at which they are affected by and recover from disturbance. We predicted that we would be able to detect grazing-related variability in soil stability at finer spatial resolutions (i.e. smaller 'scales') and at more spatial resolutions than we would for plant cover. For plants, we analysed percent cover of all non-native plants combined, and *Schismus barbatus* (L.) Thell. alone. The conservation and management importance of these two types of variables is that they collectively have strong influences on ecosystem structure, composition, and function — all of which are strongly tied to biological diversity (see Noon, 2003; Niemi & McDonald, 2004).

In characterizing vegetation, we focused on non-native species and emphasized *S. barbatus*, the most dominant exotic plant in the preserve, for several reasons. First, many non-native species thrive in areas with previously disturbed soil surfaces, and they thus can indicate edaphic conditions (Baldwin *et al.*, 2002; D'Antonio & Meyerson, 2002). Second, their increasing dominance alters soil chemistry, water balance, and fire regime (Brooks, 1999; Brooks & Esque, 2002; D'Antonio & Meyerson, 2002). Finally, they can pre-empt reestablishment of native species following disturbances such as fire and therefore govern the composition of other plants (Brooks, 1999, 2002). For example,

in the Mojave Desert, the ecological impacts of *Schismus* spp. and other alien plants include: (1) reduction of biomass and species richness of natives, even after covariates such as disturbance and soil-nutrient levels are accounted for (Brooks, 2000); (2) facilitation of the spread of fire (Brooks, 1999) and increases in fire frequency (Brooks & Esque, 2002); (3) facilitation of establishment of secondary plant invaders; and (4) allelopathic and other competitive effects on neighbouring plants (reviewed in D'Antonio & Meyerson, 2002).

With respect to soils, we focused on soil aggregate stability because repeated hoof action of non-native grazers can reduce soil-aggregate stability (Weltz *et al.*, 1989). The reduction of stability, in turn, increases the risk of wind and water erosion (Herrick *et al.*, 2001). Butler (1995) commented that very few studies had quantitatively investigated edaphic consequences of small-scale variability in herbivore use of a landscape.

Using information-theoretic analyses, we compared the ability of numerous competing models, which postulated variability in our responses at within-piosphere and landscape-level spatial scales, to describe dynamics in each of our two groups of response variables. In addition to these two primary scales of our hierarchical analyses, we evaluated the importance of grazing intensity and years since removal for soil stability at a third, finer resolution — within bare spaces only vs. vegetated and bare areas in a locale. We investigated temporal variability not only by evaluating effects of years since removal of grazers, but also by assessing responses in an abnormally dry and an abnormally wet year.

METHODS

Context and study area

Mojave National Preserve (hereafter, MNP), established as a National Park Service unit in 1994 through the California Desert Protection Act, encompasses 0.61 million ha of the eastern Mojave Desert of North America (Fig. 1). Before its designation, the land was managed by the Bureau of Land Management. Elevations within the preserve range from 85 to 2417 m. Much of MNP is managed as a wilderness area. Nonetheless, cattle grazing has occurred in this area since the 1860s. Little regulation of grazing intensity or seasonality occurred until imposition of the Taylor Grazing Act of 1934. After 1934, cattle grazing continued year-round in many habitats, with rotation of animals achieved by grazing permittees turning water sources on and off over time. As of 1999, cattle were grazing 80% of MNP.

In addition, burros (*Equus asinus* L.) have occurred in MNP and likely became feral in the Mojave Desert during the 19th century (F.H. Wagner, pers. comm.). Although burros consume both woody and herbaceous plants, for simplicity, here we refer to burros and cattle collectively as 'grazers' and their activity as 'grazing'. At our sites, however, cattle were by far the dominant ungulate. Cattle dung pats were over 35 times more abundant in belt transects than were burro dung piles across MNP. The average density of ungulate defecations in our study locations ranged from 0 to 139 defecations/100 m².

In 2001, we established permanent transects around sampling points at five water troughs (hereafter 'wells') in two adjacent allotments and added sampling at an additional five wells in 2002 (Fig. 1). Due to the perceived impacts of their grazing on the federally threatened desert tortoise (*Gopherus agassizii* Cooper), essentially all non-native ungulates (burros and cattle) were removed from the Kessler Springs allotment after our 2001 sampling, and from the Valley View allotment after our 2002 sampling (Fig. 1). When measurements occurred in 2002, grazers had been removed for *c.* 1 year from five wells, but grazing continued at the other five. When remeasured in 2003, five wells had been free of grazers for 2 years, while the other five had been free of grazers for 1 year.

We selected only wells that: (1) occurred within the two dominant vegetation communities of the preserve, bursage-creosote bush (*Ambrosia dumosa* (A. Gray) Payne — *Larrea tridentata* (DC.) Cov.) and Joshua tree-blackbrush (*Yucca brevifolia* Engelm. — *Coleogyne ramosissima* Torrey); (b) had similar soils (i.e. measured soil properties such as colour, texture, depth, and effervescence) and vegetation (i.e. the same dominant or codominant woody species) within a 1600-m radius of the well; (c) received use by cattle; and (d) were located near one or more roads, to facilitate resampling. Elevations ranged from 855 to 1420 m across the 10 wells, but the range of elevations within the 1600-m radius of each well averaged only 76 m. Precipitation at elevations of our sampling locations averaged 9–21 cm year^{-1} during the last half of the 20th century (Western Regional Climate Center weather-station data, www.wrcc.dri.edu), and soils are sandy loams (averaging within wells 50–83% of the non-gravel fraction as sand).

Sampling design

Before cattle were removed, densities of defecations and allotment-level stocking data (differing by 10–40% among seasons and years) suggested that grazing densities were similar in the two allotments. We used distance from water as a surrogate for long-term grazing intensity (*sensu* Andrew, 1988), and sampled three points at each of three distances (100, 400, and 1600 m) from each well (Fig. 1, within-well scale). For the three points 100 m from each well, we used a random-number generator to select azimuths from the well, along which we measured 100 m to place the point centre (filled circle in 'within-well scale' portion of Fig. 1). At 400 m and 1600 m from the well, we placed three points within 50–150 m of roads open to vehicular traffic to facilitate resampling (Fig. 1). Given the wilderness designation, road density (0.0055 km km^{-2} for paved and currently improved dirt roads, 69% of which is paved) in MNP is relatively low. We confirmed the 400-m and 1600-m distances from the well with a GPS unit.

Transect measurements

We obtained elevation and geographical position of all transect endpoint stakes using a GPS unit. We measured slope, aspect, and topographical position at all points to evaluate whether

response values at points were affected by these covariates. Soil samples from the uppermost 15 cm at each of ≥ 4 randomly located positions within each point were mixed. These composite samples underwent textural analyses (Soil and Plant Analysis Laboratory, BYU, Provo, UT, USA) using a 2-mm sieve to quantify proportion of the sample that was coarse material and using the hydrometer method for the remaining material (sand, clay, and silt).

Cover of *S. barbatus* and all non-native plants combined was assessed using two 50-m line-point intercept transects (Herrick *et al.*, 2005) per point. Beginning at the 1-m mark on each transect, we dropped a long pin vertically to the ground at each metre mark, thus providing 100 measurements per point. We recorded each unique plant species that touched the pin. We followed taxonomy and species authorities of Baldwin *et al.* (2002).

The soil-stability test provides information on the degree of soil-particle aggregation and erosion resistance for an area, according to the proportion of structural integrity lost in the soil fragment over time (Herrick *et al.*, 2001). This test assesses the ability of soil aggregates to remain stable when exposed to rapid wetting. At regular locations along each transect, the microsite perpendicular to the line and located 5 cm into the area left of the transect line was sampled for soil stability. We sampled at the 15-, 30-, and 45-m points along each transect, unless it was necessary to sample the nearest (perennial) vegetated microsite to these locations (most often at lower-elevation, sparsely vegetated wells) to accurately characterize both bare and vegetated microsites. At each measurement location, we recorded the soil surface cover (bare [which included annual plants], perennial grass, or shrub canopy) and took two soil fragments. These fragments, each 2–3 mm thick by 6–8 mm in diameter, included a surface sample and a sample 2.5 cm below the soil surface ('subsurface'). The surface measurements occurred on the uppermost 0.3 cm of the soil. This portion is the most sensitive to hoof disturbance by ungulates but is also the location where recovery of soil stability begins (e.g. by incorporation of soil organic matter, formation of soil crusts, etc.). Subsurface measurements reflect stability of the soil once topsoil has been disturbed or lost (Herrick *et al.*, 2001, 2005). Because stability under perennial grasses vs. under shrubs did not differ meaningfully within points across MNP in any year, these measurements were pooled. Whereas bare-ground values for stability simply reflected the mean of all measurements in interspaces at a point, the (bare+vegetated) value reflected the means of the two respective surface-cover types, weighted by amount of (measured) perennial cover at that point.

We used belt transects to measure density of defecations of burros and cattle, as well as abundance of each non-native plant species, in a 2 × 50 m area adjacent to each line transect by using a 2-m section of PVC pipe held perpendicular to the transect line. If counts of non-native plants surpassed 100, we used the count within a 0.5–5.0 m length (i.e. subportion) of the belt (dependent on density; shorter at greater densities) to estimate abundance into classes (100–500, 500–1000, and > 1000). The observer walked slowly along the middle of the belt and counted both cattle and burro defecations within the belt, accounting for instances where animals defecated while moving. Given that social structure and individual matriarchal behaviour can influence movements of grazers, abundance of animal defecations provides a more direct and spatially fine-grained measurement of recent grazing intensity than does distance from water. Distance from water, in contrast, provides a surrogate measure of accumulated grazing intensity over many years. We compared defecations to distance (see below) to see which metric better explained spatial patterns in our response variables.

Analysis

Hierarchical linear models (Bryk & Raudenbush, 1992) form a special class of statistical linear models that address multilevel structures of data. Through these models, researchers investigate how large-scale characteristics influence finer-scale relationships within their contexts. These models are also known as random-effects models (cf. Laird & Ware, 1982) or random-coefficients regression models (cf. Rosenberg, 1973). Our data formed a natural hierarchy. We developed models of the relationship of our responses (soil stability and plant cover) to measures of grazing intensity and/or clay content within each well (level 1, Appendix S1). Our models then asked whether the nature (i.e. slope and intercept) of the relationship varied systematically with factors acting at the landscape level, such as elevation or years since removal of grazers (Appendix S1, Table 1). We chose our covariates based on previous research works (Brooks, 2000; Herrick *et al.*, 2001; Brooks & Esque, 2002; Brooks & Berry, in press). Within each year, each point constituted a sample for the level 1 (within-well) models, whereas each well constituted a sample for the level 2 (landscape-level) models (Appendix S1).

We limited our hierarchical analysis to 2002 and 2003, those 2 years in which all 10 wells were sampled. Total precipitation in the 12 months before 2002 sampling was approximately half of that before 2003 sampling (Western Regional Climate Center online data, Reno, NV, USA). To account for the effect that this interannual variability in precipitation would have on plant cover, we analysed the data by including year as a fixed effect and compared removal histories only within each year. Because notable deterioration in defecation integrity occurred between our 2002 and 2003 sampling periods, for all analyses we used 2002 values for defecations at each point, to standardize our measure across sites. In this analysis, we were interested in examining relationships between grazing intensity (and other covariates) and our response variables over time and at within-well and landscape resolutions rather than any null hypothesis. Consequently, we evaluated the strength of evidence of each a priori model using an information-theoretic approach, as described by Burnham and Anderson (2002). All intervals presented in Results represent 95% confidence intervals for the reported parameters.

We developed two sets of models. The first set modelled soil stability for both surface and subsurface samples, at both bare-soil microsites only and at bare plus vegetated sites combined. The second set modelled cover of non-native species — *S. barbatus* alone and cover of all non-natives combined. In both sets, we used Akaike's information criterion adjusted for small sample

Soil-aggregate stability		Cover of non-native plants	
Within-well factors	Landscape-level factors	Within-well factors	Landscape-level factors
Grazing intensity†	Year (2002, 2003)	Grazing intensity†	Year (2002, 2003)
% clay (soil texture)	Removal status‡		Elevation
			Year * Elevation
			Removal status‡
			Elevation * Removal status

Table 1 Variables used in hierarchical analyses to describe variability in soil stability and cover of non-native plants at two spatial resolutions. Within-well factors (level 1 of Appendix S1) describe finer-resolution variability within the piosphere

†defined as either number of defecations per 100 m² or distance (in m) from water;
‡defined as number of years since grazers were removed (1, 2, or still being grazed).

sizes (AIC$_c$) to compare the evidence in support of proposed models that contained subsets of within-well and landscape-level factors from Table 1. The AIC$_c$ value of a model reflects the fit of the collected data to the model while penalizing for having unnecessary parameters. Models with the lowest AIC$_c$ values are considered the plausibly best within the set of proposed models. For each model, we calculated ΔAIC$_i$ as the difference between AIC$_c$ of the model under consideration (model i) and the one with the lowest AIC$_c$ value of all models. We calculated the generalized Akaike weight (w_i) of each model as an indicator of the strength of evidence that the selected best model is convincingly the best; w_i ranges from 0 to 1 and provides an effective way to scale and interpret the Δ_i (Burnham & Anderson, 2002). The sum of Akaike weights of models that include a particular factor can be used as weight of evidence of the importance of that factor. We calculated the evidence ratio as w_0/w_i, where w_0 is the generalized Akaike weight of the model with the lowest AIC value, and w_i is the generalized Akaike weight of model i. The evidence ratio is a relative measure of the evidence in favour of the best model vs. model i (Burnham & Anderson, 2002). Model structure for both groups of variables is detailed in Appendix S1.

In these models, the response is modelled as a linear function of grazing intensity as measured either by number of defecations at a point or by the distance of the point from water. We hypothesized that soil stability would decrease and cover of *S. barbatus* would increase with increasing grazing intensity during grazing (more defecations or less distance from water; level 1 model), but that the strength of this relationship (i.e. steepness of slope) would be smaller within a year following the removal of cattle or with longer time since removal (level 2 model). For all response variables, we modelled effect of distance as the log(distance), which approximates the exponential-decay response found for some response variables with increasing distance from water (e.g. Andrew, 1988). We sought to maximize spatial replication across MNP (i.e. number of wells sampled) and thus limited ourselves to three distances per well; however, future work may explore the explanatory power of various forms of within-well relationships.

We developed 25 a priori models for soil stability and 28 a priori models for percentage cover of non-native plants (listed in Appendix S2). Models contained specific combinations (or interactions) of abiotic covariates, measures of grazing intensity, and time since removal of grazers that we sought to compare. An
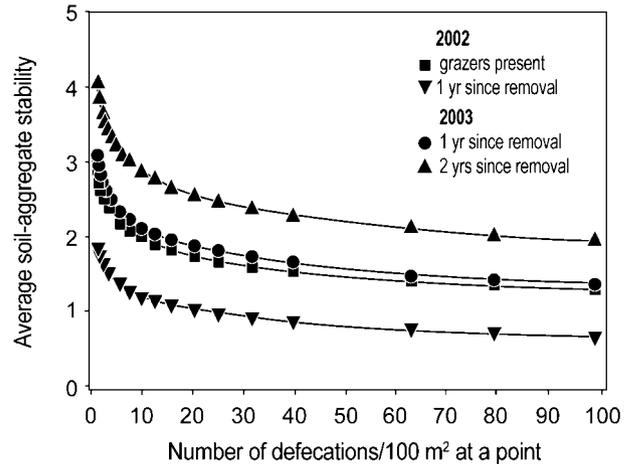
Figure 2 Changing relationship of percentage cover of *Schismus barbatus* to distance from the well with time since removal of grazers, in 2002 (grazed vs. 1-year removal) and 2003 (1-year vs. 2-year removal). Although we used a log-log scale for our modelling and hierarchical analyses, we present in all figures the back-transformed values. We sampled only at distances of 100, 400, and 1600 m; however, the modelling of this continuous variable allowed estimation of intermediate values.
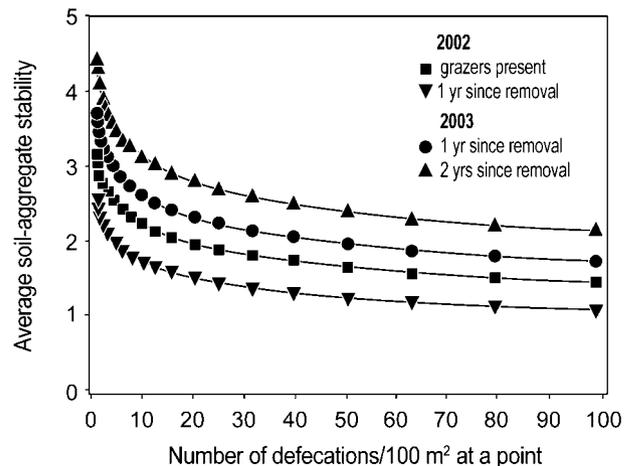

Figure 3 Changing relationship of percentage cover of all non-native plants to number of defecations (our surrogate of recent grazing intensity) over time since removal of grazers, in 2002 and 2003 (log-log scale).

Table 2a Results of AIC$_c$ analyses that compared competing a priori models that asserted variability in soil-aggregate stability was associated with grazing intensity (defecations or distance from the well), time since grazing removal, and other covariates at within-well and landscape spatial scales. Following Burnham and Anderson (2002), we sorted the models by Δ_i and report all models with $\Delta_i < 6$ and Δ_i less than the null model, plus the null model. The various models listed in the 'Model' column are explained in Appendix S2. A '+' indicates the inclusion of more than one main effect, whereas '*' indicates an interaction. 'Def' = number of defecations/100 m^2 at the point. 'Remove' = number of years since removal of grazers (still grazed, 1 year, or 2 year). 'Year' = 2002 or 2003. 'Elev' = elevation of the point, in m. Other column headings are defined in the text. Number of parameters includes main effects, interactions, and error terms, and reflects the corresponding subset of variables from either of the two two-level hierarchical models in Appendix S1 that is indicated in the 'Model' column

Model no.	Model	No. of parameters	$-2 * \log(L)$	AIC$_c$	ΔAIC$_c$	Akaike weight	Evidence ratio
Surface soil stability, bare + vegetated combined							
7	Def + Remove	9	35.4	54.7	0.0	0.45	1.00
5	Def + Year	7	42.0	56.8	2.1	0.15	2.89
19	% Clay + Def + Remove	10	35.3	56.9	2.2	0.15	3.03
8	Def * Remove	10	37.0	58.6	3.9	0.06	6.98
6	Def * Year	8	41.7	58.8	4.1	0.06	7.62
17	% Clay + Def + Year	8	41.7	58.8	4.1	0.05	7.65
1	Null	3	102.6	108.7	54.0	0.00	$> 10^6$
Surface soil stability, bare (interspace) microsites only							
7	Def + Remove	9	110.9	130.0	0.0	0.47	1.00
8	Def * Remove	10	110.2	131.6	1.6	0.21	2.21
19	% Clay + Def + Remove	10	110.3	131.7	1.7	0.20	2.34
20	% Clay + Def * Remove	11	109.9	133.7	3.6	0.07	6.18
1	Null	3	163.0	169.2	39.2	0.00	$> 10^6$
Subsurface soil stability, bare + vegetated combined							
5	Def + Year	7	53.7	68.5	0.0	0.26	1.00
4	Def	6	56.2	68.8	0.3	0.23	1.14
17	% Clay + Def + Year	8	52.9	70.0	1.5	0.12	2.09
16	% Clay + Def	7	55.5	70.3	1.8	0.10	2.47
6	Def * Year	8	53.5	70.5	2.0	0.09	2.73
7	Def + Remove	9	52.4	71.7	3.2	0.05	4.94
18	% Clay + Def * Year	9	52.7	72.1	3.5	0.04	5.82
19	% Clay + Def + Remove	10	51.6	73.3	4.7	0.02	10.74
1	Null	3	72.4	78.6	10.1	0.00	154.84
Subsurface soil stability, bare (interspace) microsites only							
2	Year	4	122.5	130.7	0.0	0.12	1.000
1	Null	3	124.8	130.9	0.2	0.11	1.089

alternative single-scale approach to analysing data from our research design would involve repeated measures, with distances from water repeated across each of the 10 wells. This approach cannot ascribe variability across the landscape in the within-well effects to any broader scale factor (such as elevation or grazing-removal status). Consequently, investigators are left able only to either estimate the average within-well effect of distance across the study area, or restrict inference to only within one to several piospheres.

RESULTS

Soil-aggregate stability

Within points, soil stability of both surface and subsurface samples was higher at sampling locations under perennial vegetation than in bare interspaces across the preserve in each year

(Wilcoxon signed rank test, $Z \leq -4.76$, $P \leq 0.0001$ for subsurface and $Z \leq -2.95$, $P \leq 0.003$ for surface).

Surface soil stability in bare and vegetated locations combined and in bare interspaces alone was clearly related to recent grazing intensity measured by ungulate defecation density (Tables 2a and 3). Time since removal of grazers clearly affected surface soil stability in bare interspaces alone, and this measure of soil stability had the most evidence of the four measures to indicate that the relationship to defecations changed with removal status (29% vs. 1–9%, Table 3). Surface soil stability was estimated to decrease between 16 and 22% for every 10-fold increase in the number of defecations, regardless of whether the measurement was taken from bare spaces only or bare and vegetated spaces combined (Figs 2 and 3). In contrast to what we anticipated, 2002 surface soil stability in bare and vegetated plots combined was 0–29% less at wells where cattle had been removed for 1 year compared to wells where cattle were still grazing. Similarly, surface

Table 2b Results of AIC_c analyses for response variables related to non-native plants. 'Dist' = ln (distance in m from water [the well]). All other column headings and variables defined as in Table 2a

Model no.	Model	No. of parameters	$-2 * \log(L)$	AIC_c	ΔAIC_c	Akaike weight	Evidence ratio
Cover of *Schizmus barbatus*							
27	Dist * Elev + Dist * Remove	14	409.8	440.6	0.0	0.70	1.00
28	Dist * Elev * Remove	19	399.9	443.1	2.6	0.19	3.59
1	Null	3	476.0	482.1	41.6	0.00	$> 10^6$
Total cover of all non-native plants							
14	Def * Remove + Elev * Remove	14	331.6	362.4	0.0	0.24	1.00
11	Def * Remove	12	336.5	362.5	0.2	0.22	1.08
6	Def * Year	8	345.7	362.7	0.3	0.21	1.14
15	Def * Elev + Def * Remove	13	335.5	363.9	1.5	0.11	2.17
8	Def * Elev * Year	9	345.3	364.4	2.1	0.09	3.28
27	Dist * Elev + Dist * Remove	15	332.8	366.0	3.6	0.04	5.99
1	Null	3	418.2	424.4	62.0	0.00	$> 10^6$

Table 3 Sum of Akaike weights for each of several factors related to grazing regime, for each variant of our two response variables. Factors are defined as in Appendix S2. 'Def' = ln (number of defecations/100 m^2), and reflects recent grazing intensity. 'Remove' denotes number of years since grazers were removed (still grazed, 1 year, or 2 years)

Response variable	Def	Distance from water	Remove	Interaction of remove with Def or Dist
Soil stability				
Surface, bare and vegetated	0.996	0.004	0.700	0.088
Surface, bare only	0.998	0.002	0.963	0.291
Subsurface, bare and vegetated	0.980	0.016	0.100	0.018
Suburface, bare only	0.264	0.252	0.242	0.010
Cover of non-native plants				
S. barbatus	0.043	0.957	0.940	0.932
All non-native species	0.920	0.080	0.690	0.666

soil stability in only bare interspaces in 2002 was 11–39% less at wells where cattle had been removed for 1 year compared to wells where cattle were still grazing (Fig. 2). In 2003, surface soil stability in bare and vegetated areas combined was similar for wells from which cattle had been removed 1 year vs. 2 years before. However, as we predicted, surface soil stability in only bare areas was 3–50% higher at wells from which cattle had been removed 2 years compared to wells where cattle had been removed only 1 year (Fig. 2).

Although subsurface soil stability in bare and vegetated interspaces combined was also clearly related to recent grazing intensity, subsurface soil stability in bare interspaces alone was essentially constant throughout the study area and not detectably related to any of our proposed explanatory factors (Tables 2a and 3). There was little evidence to indicate that either metric of subsurface soil stability was related to time since removal of grazers, and no evidence to suggest that the relationship to grazing intensity varied with removal status (Table 3). Subsurface soil stability in bare and vegetated interspaces combined was estimated to decrease between 3% and 23% for every 10-fold increase in the number of defecations.

Cover of non-native plants

Cover of *S. barbatus* was strongly related to distance from water, and this relationship changed with elevation and years since removal of grazers (Tables 2b and 3; Fig. 4). As elevation increased, the relationship of *S. barbatus* cover to distance from the well became more negative. For every 100-m increase in elevation and 10-fold increase in distance, *S. barbatus* cover was reduced between 14% and 29%. In 2002, at wells where cattle were still grazing, *S. barbatus* cover did not change with distance; however, for wells from which cattle had been removed, *S. barbatus* cover increased between 1.8- to 6.3-fold for every 10-fold increase in distance. In 2003, *S. barbatus* cover was similar for wells from which cattle had been removed 1 or 2 years before, and was estimated to decrease between 39% and 64% for every 10-fold increase in distance from water (Fig. 4).

Cover of all non-native plants (and nearly all other annuals and biennials) appeared to strongly track precipitation between the 2 years, and exhibited much higher cover at points across MNP in 2003 (range 6–86%, mean ± 1 SE = 37.0 ± 2.4) than in 2002 (range 0–16%, 4.1 ± 0.4). Nonetheless, non-native cover at
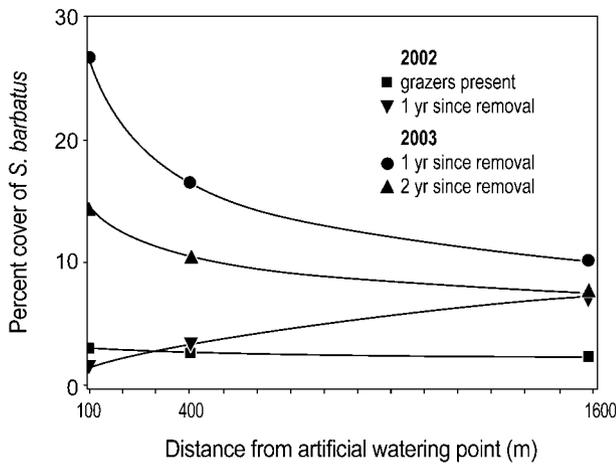
Figure 4 Relationship of (soil-aggregate stability of surface samples in bare interspaces) to number of defecations as a function of time since removal of grazers and year.
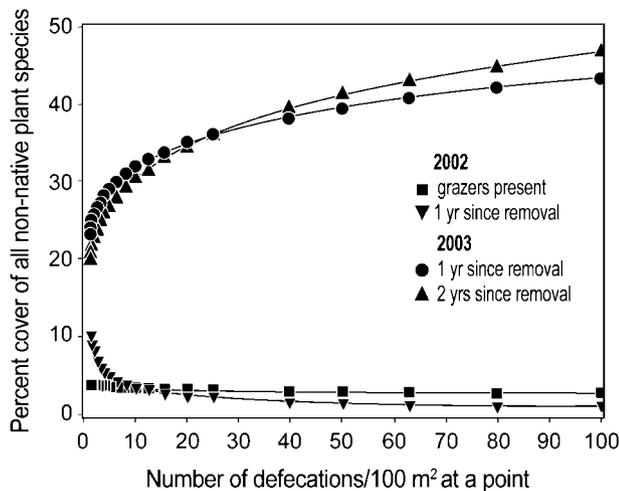

Figure 5 Relationship of (soil-aggregate stability of surface samples, across bare and vegetated microsites) to number of defecations as a function of time since removal of grazers and year.

points averaged only 15.2% (range 5–33%) in 2001, when grazing remained. This pronounced increase in total non-native cover from 2001 to 2003 occurred despite the fact that precipitation at the closest weather station averaged 19% greater in the 12 months before 2001 sampling when grazing was still occurring, compared to the 12 months before 2003 sampling when grazers had been removed 1–2 years (Western Regional Climate Center, online data).

Both the top-ranking model and total Akaike weights for cover of non-native species indicated that the relationship of non-native species cover to recent grazing intensity changed with years since removal of grazers and elevation (Tables 2b and 3; Fig. 5). In 2002, at wells where cattle were still grazing, cover of non-native species did not change with number of defecations. However, for wells from which cattle had been removed for 1 year, non-native species cover decreased between 52% and 66%

for every 10-fold increase in the number of defecations. In 2003, cover of non-native species was similar for wells from which cattle had been removed 1 year or 2 years before, but now was estimated to increase between 1.1- and 2.0-fold for every 10-fold increase in the number of defecations (Fig. 5). As for soil stability, models with defecations comprised most (92.0%) of the total weight for cover of all non-native plants (Table 3).

DISCUSSION

Disturbance and ecosystem response to disturbance involve an array of processes, each of which operates on its own spatial and temporal scale. For example, grazing by ungulates such as cattle and feral burros involves processes of nutrient redistribution, selective forage consumption, and trampling of soils and plant parts. Relative to our response variables, ecosystem response to such grazing may involve frost heaving and freeze–thaw cycles in soils, development of biological soil crusts, and succession of the plant community resulting from episodic dispersal and establishment (Archer & Smeins, 1991; West, 1993). Given the spatial and temporal heterogeneity that exists at several scales within ecosystems and the forces that shape them (Gimona & Birnie, 2002; Kie *et al.*, 2002), numerous authors (e.g. Palik *et al.*, 2000; George & Zack, 2001) have argued that landscape hierarchies and scale considerations should guide restoration efforts for both plant communities and vertebrate species.

In terms of grazing disturbance, spatial heterogeneity in plant and soil resources has a profound effect on how herbivores utilize a given landscape, at each of several spatial resolutions (Archer & Smeins, 1991; Kie *et al.*, 2002). In our work, for example, defecation density averaged higher at points 1600 m from water than at 400-m points at 70–80% of our wells. This reflection of recent grazing patterns differs from the generally observed phenomenon over longer timescales of exponentially decreasing use by grazers with increasing distance from water (e.g. Andrew, 1988). Several authors have found that heterogeneity in grazing intensity can, in turn, modulate changes in primary productivity after grazing (Semmartin & Oesterheld, 2001) and differentially affect soil-crust populations (Rogers & Lange, 1971) and numerous edaphic properties (Reichman *et al.*, 1993; Butler, 1995).

In our work, we observed heterogeneity in grazing disturbance and ecosystem recovery at several spatial resolutions. At the finest scale, we found greater importance of time since grazer removal for soil stability in surface than in subsurface samples, although this effect of removal could only be interpreted as recovery in the wetter year (2003). We also observed higher soil stability under perennial vegetation than in bare spaces and found different dynamics governing soil stability in bare spaces alone compared to bare and vegetated spaces combined (Tables 2a and 3). Furthermore, we detected in all our response variables within-well gradients that were related to recent or long-term grazing intensity. Finally, we noted the importance of landscape-level variables such as elevation and grazer-removal status for all our response variables (Table 2, Figs 2–5). The only exception for these last two phenomena was subsurface soil stability in bare spaces, which was unrelated to any of our predictors. In systems

still being grazed, the creation of such herbivore-induced gradients in soils and vegetation may enter into positive feedbacks with how herbivores utilize the landscape, thus magnifying the change in patterns of resource alteration. Following herbivore removal, however, ecosystem response can be modulated not only by heterogeneity in plant species composition and past herbivore densities, but also by variation in forage preferences, soils, climate, and other disturbances such as fire (Ryerson & Parmenter, 2001).

Adler *et al*. (2001) observed that the scale of observation was critical in determining whether grazing patterns were stronger or weaker than vegetation patterns, or mirror spatial structure of vegetation. Others have similarly suggested that the scale of investigation fundamentally affects the ability of investigators to detect effects of non-native species on ecosystem function (D'Antonio & Meyerson, 2002) and many other ecological phenomena. Our approach allowed us to produce interpretations about response to disturbance at several spatial resolutions, yet replicate that understanding across a broad landscape extent. The need for such multiscale investigations is underscored not only by the paucity of research on grazing in the Mojave Desert (Lovich & Bainbridge, 1999; Boarman, 2002), but also because spatial pattern may affect ecological outcomes of disturbance (Kallimanis *et al*., 2005) and restoration (Maestre *et al*., 2003) of habitat.

Soil-aggregate stability

Ungulates are more likely to walk on and trample interspaces than areas under vegetation (Balph & Malechek, 1985), and effects of their hoof action are attenuated as soil depth increases. Given the former, our finding across years of significantly higher soil stability under vegetation compared to in bare interspaces matched our prediction. In addition to differential trampling between the two types of sampling locations, amount of vegetative cover may compound these differential impacts by protecting soil structure under canopies from direct raindrop impact (Thurow *et al*., 1986). Given the latter phenomenon (i.e. attenuation), the fact that one of our subsurface soil-stability metrics related to none of our explanatory variables (Table 2a) is not surprising.

When both the tendency of grazers to trample bare interspaces and the soil-depth attenuation are considered, and combined with the fact that recovery of soil structure begins at the surface (where organic material is deposited and microbiotic crust formation begins), one would predict that soil stability would be most sensitive to grazer impacts and quick to recover in surface samples from bare interspaces. Accordingly, the only variant of stability in which the defecations-by-removal variable was among the plausible best models was for surface samples in bare spaces (Table 2a). The defecations-by-removal variable indicated that the relationship of stability to grazing intensity (no. of defecations) changed with grazing status (grazed vs. 1 year removed, 1 year vs. 2 years removed). Although soil stability was higher in 2003 than in 2002, the legacy of past grazing impacts (i.e. the relationship to increasing numbers of defecations) remained,

even 1–2 years after grazers had been removed (Figs 2 and 3). Surface soil stability in bare spaces was 3–33% less at wells from which grazing had been removed 1 year vs. 2 years in a wet year, as we predicted. However, comparisons of the same wells in a dry year (2002) showed stability of surface samples to be higher at grazed points compared to those from which grazers had been removed 1 year. This kind of temporal variability is characteristic of low-productivity, event-driven systems such as the Mojave Desert, and was observed more dramatically in cover of non-native plants.

Soil stability appeared to be better predicted by finer-resolution variability in recent grazing intensity (i.e. number of defecations) than longer-term, cruder indices of grazing intensity (distance from water) that best predicted *S. barbatus* cover (Tables 2 and 3). The relative strengths of these relationships are consistent with the mechanisms of disturbance and recovery of those variables. Soil stability relates directly to the mechanical processes of ungulate trampling and particle reorganization. In contrast, cover of *S. barbatus* is influenced not only by changes in the physical and chemical properties of soil, but also requires the longer-term processes of seed dispersal and germination, and seedling establishment.

Cover of non-native plants

Given the effects that trampling by ungulates can impose on soil surfaces and herbaceous (including non-native) vegetation (Rogers & Lange, 1971; Butler, 1995), an ephemeral spike in cover of non-native and ruderal plants after removal of livestock grazing matched our prediction. Over longer timescales, this spike may be followed by a more protracted replacement of those ruderal species by longer-lived species. Within this desert ecosystem, the replacement of annuals with an equal cover of perennials seems unlikely, because perennial vegetation is often widely spaced in such arid, low-primary-productivity environments. If annual plant cover has not risen high enough to cause a threshold to be crossed (e.g. loss over time of perennial seed sources, increased fire frequency), then establishment of perennial vegetation and its competition for resources will likely reduce the dominance of annuals. Whereas one model of *S. barbatus* cover was clearly the best among those we proposed, there was no clear best model for describing total non-native plant cover, which represents a mix of many species life histories (Table 2b). Despite this difference, all of the plausible best models for these two plant-cover variables nonetheless contained both local- and landscape-scale variables (Tables 1 and 2b).

The relationship of *S. barbatus* cover to distance from water became increasingly negative with increasing elevation. This same relationship was also found in our 2001 data when grazers were still present; the distance-by-elevation model was the only plausible best model out of a subset of nine proposed models. At highest elevations of our sampling, cover of *S. barbatus* decreased with increasing distance from the well. This was in contrast to *B. rubens*, which exhibited lowest abundance in 100-m belt transects at all wells at which it was present (data not shown). It remains unclear from our study whether the change across

elevations in the slope of the relationship of *S. barbatus* to distance from water reflects competition with *B. rubens*, autecological variation related to the species ecological (or physiological) niche, or both phenomena.

Detecting heterogeneity in response to disturbance and its removal

Spatial heterogeneity in the distribution of grazing impacts results not only from the spatially variable pattern of landscape use by herbivores at multiple resolutions (Adler *et al.*, 2001; Augustine & Frank, 2001; Semmartin & Oesterheld, 2001; Teague *et al.*, 2004), but also from the differential vulnerability of various portions of the landscape to ungulate grazing (Milchunas & Noy-Meir, 2002; Harrison *et al.*, 2003). This latter phenomenon may result from heterogeneity in soil types and soil properties, physical impedances to grazing (which create refuges, exemplified in our work [E.A. Beever, unpublished data] by the areas under shrubs protected by spines and thorns), and competitive-neighbour influences. These two sources of variability in turn interact with landform (topography), climate, and other disturbances to modulate not only effects of grazing disturbance across the landscape but also response to grazing removal (Stohlgren *et al.*, 1999; Ryerson & Parmenter, 2001). Through careful site selection and accounting for covariates such as elevation and (less commonly) percentage clay, we were able to examine the effects of several possible sources of variability.

Investigators have resoundingly called for monitoring, restoration, and conservation effort to occur at multiple spatial resolutions and extents (West, 1993; George & Zack, 2001; Brooks & Esque, 2002; Noon, 2003; Niemi & McDonald, 2004), with consideration of background heterogeneity (Beatley, 1969; Harrison *et al.*, 2003). In fact, many authors have noted that phenomena were not detected because either the extent or the resolution of the investigation was not properly chosen (May, 1994; Kepner *et al.*, 2000). Accordingly, although fully one-fourth of our candidate models asserted that variability in the response variable was attributable to only one spatial resolution (within-well or among-wells), all 18 models with $\Delta_i < 6$ for non-native plant cover and surface soil stability contained factors from both the within-well and the landscape-level resolutions. Thus, this suggests that non-hierarchical investigations would provide an incomplete understanding of the dynamics of these (and likely many other) variables.

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SUPPLEMENTARY MATERIAL

The following material is available online at
http://www.blackwell-synergy.com/loi/ddi

Appendix S1 Structure of hierarchical linear models for cover of non-native plants (*Schismus barbatus* alone, as shown below, or all non-native species combined) and soil-aggregate stability.

Appendix S2 List of competing *a priori* models analysed with hierarchical linear models, data from 2002 and 2003. "Def" refers to the average number of ungulate defecations per 100-m^2 belt transect at each point.