

WOODY PLANT DYNAMICS IN A SONORAN DESERT ECOSYSTEM ACROSS
SCALES: REMOTE SENSING AND FIELD PERSPECTIVES

by

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SIGNED: Dawn M. Browning

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DEDICATION

To my mother, Isabel Louise Browning, who instilled strength and encouraged me to reach for the stars. This is for you.

and

To William McGinnies and George Glendening. Their hard work, legacy, and demonstrated altruism are exceptional – then and now.

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ABSTRACT

Historic land uses impose discernable legacy effects that may influence ecosystem function, a concern of particular importance in actively managed landscapes. In recent history (ca. 150 years) tree and shrub abundance has increased at the expense of native grasses in savannas and grasslands. The magnitude and patterns of change are spatially heterogeneous, highlighting the need for analytical approaches spanning multiple spatial scales, from individual plants to patches to landscapes. The overarching goal of this dissertation was to explore long-term dynamics associated with woody plant encroachment with aerial photography and field studies to examine cover, density, soils and land use history at the Santa Rita Experimental Range.

The first study characterized patterns in woody cover change on contrasting soils over 60 years using aerial photography. Woody patch dynamics revealed encroachment and stabilization phases in woody plant proliferation. Soil properties reflected the rate at which uplands reached a dynamic equilibrium, but not the endpoint (ca. 35% cover). Fluctuations around dynamic equilibrium reflected net change in patch growth and acquiescence combined with colonization and mortality. Efforts to characterize changes in land cover will require patch-based assessments beyond coarse estimates of percent cover.

The second study capitalized on historic field measurements of shrub canopies to validate estimates of shrub cover derived from the earliest aerial photography, quantified detection limitations of 1936 aerial photographs for mapping shrub cover, assessed species-specific contributions to percent cover, and translated detection limitations to

proportions of velvet mesquite (*Prosopis velutina* var *Woot.*) biomass missed with 1930s aerial photography.

The third study was a field-based approach investigating how livestock grazing influenced mesquite cover, density, biomass, and stand structure over 74 years. The study supplemented traditional statistical analysis of grazing effects with methods quantifying spatial autocorrelation structure of mesquite density by grazing treatment. The outcome re-affirmed the supposition that mesquite cover may be dynamically stable at ca 30%, and revealed that livestock grazing slowed the shrub encroachment process from 1932 to 2006, counter to expectation. Results indicate that shrub growth trajectories persist long-term. Overall, this work affirms the importance of land use legacies and long-term perspectives in rangeland shrub dynamics.

INTRODUCTION

Relevance of history

Land use legacies influence current vegetation structure, restrict future responses, and represent an unknown for explaining past changes and forecasting future trends in land cover (Foster et al. 2003). Disregard for historic land uses can place short-term studies in the ‘invisible present,’ possibly yielding misleading conclusions (Magnuson 1990, Weltzin et al. 1997). Interpretations of current spatial patterns and linkages to processes that generate them are informed by knowledge of past land management activities (Peters and Havstad 2006). Livestock grazing, the most geographically extensive form of land use worldwide (Asner et al. 2004), can directly or indirectly cause changes that persist for decades (Archer 1995). In this context, footprints of historic land uses imposed upon grasslands and savannas (hereafter “rangelands”) and their effects on ecosystem function are especially relevant to management activities associated with livestock production and agricultural practices.

Woody plant encroachment

Current patterns of land cover change, shifts in land use (DeFries et al. 2004), loss of biodiversity (Singh 2002), and changes in climate (IPCC 2003) are unprecedented in modern human history. Changes in land cover and land use are principal drivers of global change (Vitousek 1992, 1994, Pielke et al. 2002). Savannas and grasslands occupy ca. 40% of the land surface (Bailey 1996), contribute 30-35% of the terrestrial net primary productivity (Field et al. 1998), and are inhabited by more than two billion

people (Safriel and Adeel 2005). One of the most striking land cover changes in rangelands worldwide over the past 150 years has been the proliferation of trees and shrubs at the expense of perennial grasses. The geographic extent of this shift in physiognomy (i.e., woody plant encroachment) has ramifications for terrestrial carbon cycling, the hydrologic cycle, land-surface interactions, and human health for a burgeoning human population.

Drivers of the shift in physiognomy in grasslands and savannas are the topic of ongoing debate (Archer 1994, Archer et al. 1995, Van Auken 2000, Briggs et al. 2005). The relative roles of land management (e.g., livestock grazing, fire suppression, and brush management) and climate in woody plant encroachment are controversial and are mediated by elevation, soil properties, and landform (Archer 1995). Many of these factors are potentially confounded, making clear assessments of their roles problematic (Archer and Bowman 2002). Only when complex interactions are taken into account, may a consensus emerge, providing a better understanding of the spatial and temporal dynamics of woody plant encroachment and the role of rangelands in the terrestrial carbon cycle. Traditional perspectives on woody plant encroachment have been centered around livestock production (e.g., Fisher 1950, Glendening 1952); and woody plant encroachment can be a significant impediment to sustainable livestock production.

When discussing effects of livestock grazing on land cover changes in arid and semi-arid rangelands, it is important to recognize that livestock represent only part of the story, for herbivory encompasses grazing, browsing, and granivory (Archer 1994). Effects of herbivory on woody cover vary according to herbivory guild and exhibit non-

linear relationships (Scholes and Archer 1997, Sankaran et al. 2008). Browsing directly (negatively) influences population structure with notable effects on seedling survivorship; granivores may promote woody plant establishment by caching or scarifying seeds (Glendening and Paulsen 1955). Grazing may promote woody plant proliferation by decreasing competition for soil water and nutrients from grasses or curtail establishment if large herbivores browse or trample emergent seedlings (Huntly 1991, Archer 1995, Scholes and Archer 1997). Livestock exhibit direct and indirect effects promoting the spread of leguminous shrubs in the Genus *Prosopis* that include seed dispersal (Archer 1994, Brown and Archer 1999), alteration of soil structure and chemistry, and reductions in fire frequency due to decreases in fine fuel loads (Archer 1996). These effects are variously expressed atop the edaphic matrix which also exerts influence over biotic interactions and shrub establishment (Archer, 1995).

Soil properties (i.e., texture, depth, and fertility), climate (amount and seasonality of precipitation), and topography interact to influence patterns and abundance of woody plants (Johnson and Tothill 1985, Knoop and Walker 1985, Walker 1987). Combined, these factors determine how surface water, a critical resource in drylands, is distributed (i.e., run-on and run-off) (Noy-Meir 1973, Tongway et al. 2001, Wilcox et al. 2003) and provide the backdrop against which biotic factors influence woody plant dynamics. Coarse-textured soils permit percolation of rainfall to greater depths, where woody plants with deeper root systems may preferentially access it. Generally, perennial grasses are senescent during winter and make use of summer precipitation. Multi-temporal assessments of cover change in context of seasonal precipitation patterns and

geomorphology (soil age and texture) may explain variable patterns in woody plant cover change across heterogeneous landscapes. Edaphic influences on woody plant cover change derived using remotely sensed imagery have been documented (Archer 1995, Hudak and Wessman 1998, Asner et al. 2003). However, the extent to which woody plant encroachment into uplands over decadal time scales has been promoted or constrained by soil properties is not widely documented, and patch-level assessments of edaphic influences on growth, fragmentation, and coalescence of shrub patches are sparse.

Few studies have simultaneously considered multiple factors (e.g., livestock grazing, fire, precipitation, and soils) known to influence woody plant dynamics, although recent advances have revealed that all of these factors contribute to observed changes in woody cover with different degrees of explanatory power (Sankaran et al. 2005, Sankaran et al. 2008). Woody plant dynamics are similarly influenced by the interactions between density-dependent regulation of woody plant stocks and precipitation (Roques et al. 2001, Fensham et al. 2005). Changes in woody plant density and cover as a function of initial conditions and climate range from high plant densities and drought frequency coinciding with shrub mortality (Roques et al. 2001) to increases in cover associated with above-average precipitation and low initial cover (Fensham et al. 2005). These findings highlight the importance of examining interactions between biotic processes regulating population dynamics and dynamic environmental cues. Numerous lines of evidence indicate woody plant cover and population structure in rangelands worldwide are density-dependent (Glendening 1952, Smith and Goodman 1986, Martens

et al. 1997, Fensham et al. 2005). To build upon this knowledge, next steps are to extend the period of observation of woody plant dynamics (beyond 50 years) and determine whether topographic conditions result in different dynamic equilibria for woody plant cover. In the first study of this dissertation, I examined edaphic influences on upland shrub dynamics over 60 years with aerial photography holding livestock grazing and climate constant (Appendix A).

Remote sensing for woody plant dynamics and biomass estimation

Remote sensing affords synoptic perspectives and availability of historic records to gauge changes over decadal time scales (Wessman et al. 2004) and is an obvious means by which to monitor changes in terrestrial biomass at large spatial scales (Huete et al. 2002, Asner et al. 2003, Wessman et al. 2004, Bar Massada et al. 2006, Lu 2006, Huang et al. 2007). Aerial photography provides fine spatial and historic perspectives required to monitor patterns in cover for long-lived woody plants. However, commercially available aerial photography may not permit delineation of individual plants in situations where canopies of adjacent individuals overlap and thus appear as single objects. Therefore, the appropriate sample unit in remote sensing analyses of woody cover change is the “patch” comprising contiguous canopies of adjacent plants. An additional constraint of using aerial photography to evaluate edaphic, topographic, and climatic influences on woody plant dynamics is the inability to capture the earliest stages of plant development. Because individuals must achieve a certain size before they are distinguishable in the imagery (based on the ground-resolved distance of the photo

series), data regarding seedling establishment and juvenile growth must come from field-based studies. As such, the use of aerial photography focuses research attention on later stages of plant development (juvenile to mature individuals). As proof of concept and means to improve efforts to monitor woody patch dynamics, in the second study, we quantified detection capabilities of early aerial photography (Appendix B).

Synoptic assessments of landscapes enable mapping of aboveground carbon stocks across large areas (Fensham and Fairfax 2002, Asner et al. 2003) and woody patch size distributions (as surrogate for age structure) have been used to represent population dynamics at the patch level (Wiegand et al., 2006; Meyer et al., 2007). In southwestern U.S. rangelands, aerial photography (as early as mid-1930s) has been used to track changes in vegetation (Goslee et al. 2003, Laliberte et al. 2004), providing the ability to examine historic changes in cover on different topographic settings.

Consideration of space

Multi-temporal landscape analyses are necessary to understand the role of historic land practices and abiotic factors (e.g., geomorphology, landform, and elevation) in the rates, dynamics, and spatial patterns of change in shrub cover. Association of ecological process with observed spatial patterns is a main focus of landscape ecology (Turner et al. 2001). It should be noted that while contributions to our understanding of ecosystem function can be made in this manner, caution should be exercised when attempting to link spatial pattern and process. It is imperative that ecologically relevant processes are considered when investigating spatial pattern, although presence of a pattern does not

necessarily imply a particular process is acting to form it. Reciprocal relationships between pattern and process should be critically examined rather than assumed (Li and Wu 2004).

Spatial structure pervades ecological data because biotic interactions and regulatory processes influence neighboring units (Wagner and Fortin, 2005). For sessile organisms such as plants, spatial associations range from positive (e.g., clusters of similar values) to negative (e.g., dissimilar adjacent values). Moran's I (Moran 1950) is a commonly used metric for contiguous data that quantifies patterns of association in a spatially explicit manner (Moran 1950, Anselin 1995). Spatial autocorrelation has notable ramifications for statistical inference by violating the assumption of independent observations and residual errors (Legendre 1993). Ecological processes act at multiple spatial scales, highlighting the need to assess patterns at local as well as broader scales of analysis. Realistic depictions of dynamic changes across complex landscapes necessitate cross-scale linkages (Hampe et al. 2008). In this manner, spatial metrics may be more sensitive to treatment effects than broad scale measures of vegetation abundance, such as percent cover.

Local anomalies in the distribution of spatial metrics may indicate pattern within neighborhoods; neighborhood-based metrics (i.e., local spatial statistics) depict spatial heterogeneity that is averaged in a global metric (Getis and Ord 1992). Local spatial statistics permit evaluation of the degree to which the global statistic represents the average pattern of local association and enhance understanding of how local patterns contribute to the global statistic (Wagner and Fortin 2005). Statistical assessments and

predictive models incorporating the functional role of spatial structure are apt to capture previously unexplained variance and improve capabilities to forecast woody stand dynamics.

In exploring the spatial patterns of vegetation response to livestock grazing, herbaceous cover has been emphasized (see Adler et al. 2001). Few studies have quantified spatial patterns of change for the woody plant component in rangelands and those rely on aerial photography to evaluate patch arrangement over time (Goslee et al. 2003, Heaton et al. 2003, Seifan and Kadmon 2006). Goslee et al. (2003) documented shrub encroachment from 1936 to 1996 with aerial photography and coupled their assessment of shrub patch dynamics with point pattern analysis to find that shrub patterns shifted from clumped (or aggregated) to random to regular (or dispersed) distributions in line with predictions suggesting competitive interactions regulate spatial pattern.

In an assessment of grazing effects on patterns in shrub distribution, Seifan and Kadmon (2006) derived shrub cover from aerial photographs in a Mediterranean scrub community to test the hypothesis that grazers, by mediating grass-shrub competitive interactions, dictate spatial patterns of woody patch development. They predicted that grazing would yield a random shrub distribution. The prediction was based on the assumption that grasses inhibit woody plant establishment and that woody plant establishment in interstitial spaces would be promoted by alleviating the inhibitory effect of grasses. Although patterns corresponded to their predictions, the presumed inhibitory nature of grasses on woody plant establishment may be too simplistic (Brown and Archer 1999). In addition, assessments of spatial patterns of shrub encroachment determined

from aerial photography fail to account for young (small) shrubs below the detection limit of the imagery and miss or misrepresent spatial patterns of individual juvenile and adult plant growing in close proximity.

Dissertation overview:

My dissertation research encompasses analyses of woody plant dynamics at a range of spatial scales in a Sonoran desert mesquite shrubland, where the dominant woody plant, *Prosopis velutina*, is known to have increased in abundance over approximately the last 100 years (McClaran 2003). The work matches remotely sensed measures of woody cover and associated patch dynamics over 60 years with field measurements of *P. velutina* structure spanning 74 years. The dissertation comprises three manuscripts in different stages of peer-review or publication.

The first research chapter (Appendix A), “Post-encroachment dynamics: Woody plants in grasslands” was published in *Ecological Applications* 18(4):928-944 and describes woody cover dynamics derived from aerial photography over 60 years on contrasting soils and combines field data to characterize patch structure and *P. velutina* biomass.

The second research chapter (Appendix B), “Field validation of 1930s aerial photography: What are we missing?” involved a unique opportunity to verify 1936 photo-derived estimates of woody cover with 1932 field data to quantify the detection limitations and ramifications for early estimates of cover and woody biomass. This manuscript is currently under review for the *Journal of Arid Environments*.

The third research chapter (Appendix C), “Disturbance, space, and time: Long-term mesquite (*Prosopis velutina*) dynamics in Sonoran desert grasslands (1932 – 2006),” represented a field perspective on the effects of livestock grazing on *P. velutina* stand structure, cover, biomass over 74 years. In addition, we calculated spatial autocorrelation structure over time to express the effects of livestock grazing on *P. velutina* recruitment patterns. This manuscript, intended for submission to *Ecological Applications* at this writing, tested the widely held opinion that livestock grazing facilitates the shrub encroachment process.

I took the lead role in these research endeavors by devising analytical approaches, compiling ancillary data used to select study sites, collecting data, performing data analyses and interpretation, and writing the manuscripts. Co-authors participated in data interpretation, assisted with study site stratification, and provided editorial oversight, and logistical and material support.

PRESENT STUDY

The unique contribution of this dissertation to the current state of knowledge are the consideration of pattern at multiple spatial scales (e.g., plants from field survey, shrub patches derived from aerial photos, and shrub cover across landscapes using aerial photos) and efforts to link field measurements to remotely-derived metrics in this assessment of dynamics associated with woody plant encroachment. I applied principles and techniques from the fields of landscape ecology, geographic information science, and remote sensing to address questions posed by researchers in the fields of plant ecology and rangeland management. I quantified dynamics of shrub cover change at multiple spatial scales while isolating the effects of contrasting soils. Spatial statistics and pattern analysis supplemented traditional statistical approaches to provide a point from which to launch focused field studies to identify mechanisms underlying velvet mesquite (*Prosopis velutina* Woot.) recruitment and stand development.

Studies conducted at broad spatial scales incur inherent challenges associated with replicating sample units (i.e., landscapes); the issue permeates the hierarchy of spatial scales (Turner 2005). The key is to examine the full range of landscape conditions when evaluating treatment effects. When capitalizing on historic field studies, replication, or the lack thereof is inherited. I contend that depth of the historic record outweighs the limitation imposed by logistical constraints associated with an exhaustive field sampling of a single plot (Appendix C). Efforts were taken to stratify landscapes by factors known to influence woody patch dynamics, thereby distinguishing replicated landscapes (Appendix A). Long-term data were subjected to quantitative measures to determine the

degree of spatial autocorrelation and select the appropriate sample size to meet assumptions for parametric statistical procedures (Legendre 1993, Appendix C). The methods, results, and conclusions of this study are presented in the papers appended to this dissertation. The following is a summary of the most important findings in the document.

Appendix A: Post-encroachment dynamics: Woody plants in grasslands

I used time-series aerial photography (1936, 1966, and 1996) and field studies to quantify cover and biomass of *P. velutina* on the Santa Rita Experimental Range (SRER). Patch-level analyses revealed two stages to the woody plant encroachment process: an encroachment phase and a stabilization phase. Additional insights gained from this study highlight challenges for estimating aboveground woody biomass by applying plant canopy-based allometric relationships to patches derived from remotely sensed imagery as well as problems with linking seasonal precipitation patterns with shrub patch development derived from aerial photography. Historic records were used to estimate rates of shrub canopy expansion to quantify the lag in growth response that renders links between shrub colonization and climate problematic. Additionally, I ascertained that soils properties (percent clay and soil depth) were related to the rate at which shrub cover reaches a dynamic equilibrium, but not the approximate end point. This realization poses important ramifications for adaptive land management as well as carbon storage potential in rangelands associated with woody plants.

Appendix B: Field validation of 1930s aerial photography: What are we missing?

On the Santa Rita Experimental Range (SRER) in southeastern Arizona, panchromatic aerial photography from 1936 serves as the earliest synoptic depiction of vegetation cover in the form of 1:31,640 black and white photographs. I capitalized on the well-documented land use history of the SRER to generate a spatially-explicit database of shrub (*Prosopis velutina*) stand structure within two 1.8-ha field plots established in 1932 to address two questions: (1) What are the detection limits of 1936 aerial photography (i.e., smallest reliably discernable *P. velutina* canopy)?, and (2) How much *P. velutina* biomass do we miss using 1930s aerial photography? Aboveground *P. velutina* biomass in 1932 plots was estimated using a site-specific allometric relationship for field-measured canopy area. Shrub canopy detection limits on the 1936 imagery proved comparable to what has been reported for more modern images. Based on a conservative shrub size detection threshold of 3.8-m² (90th percentile for plants not visible on imagery) ca. 5.8% of *P. velutina* biomass would be missed on 1936 aerial photography.

These analyses provided a basis for quantifying uncertainty associated with the woody cover estimates from the earliest aerial photography, which is often the baseline for studies of land cover change. In addition, results highlight the importance of accounting for uncertainties associated with shrub cover and biomass estimates derived from historic aerial photography.

Appendix C: Disturbance, space, and time: Long-term mesquite (*Prosopis velutina*) dynamics in Sonoran desert grasslands (1932 – 2006)

Livestock grazing is widely regarded as a factor in the shrub encroachment process (Bahre 1991, Van Auken 2000), though most evidence is circumstantial. Goals of this research endeavor were: (1) to quantify changes in the abundance and spatial distribution of woody plant cover to evaluate how livestock grazing influences *P. velutina* canopy cover, density, and above-ground biomass, and (2) to extend the long-term record of *P. velutina* abundance and distribution within study plots established in 1932 to quantify demographic patterns in mesquite over 74 years.

Research is conducted in the Sonoran desert grasslands at the SRER, a 21,514 ha (45-km south of Tucson, AZ), where increases in *P. velutina* are known to have occurred since 1900 (McClaran 2003). In May 2006, I repeated field measurements taken on woody plants in 1932 and 1948 (canopy diameter and mapped locations of individual shrubs) on a 200-m X 40-m portion of one plot centered on a livestock enclosure treatment boundary. Livestock grazing history for this site likely commenced in the 1880s, a period marked by unregulated heavy grazing pressure. The SRER was fenced out of the public domain from 1903 to 1915 (Sayre 2003). The 0.8-ha area surveyed in 2006 comprised a 100-m X 40-m (0.4-ha) area open to lagomorphs and livestock since 1916 (hereafter, “grazed plot”) and a 0.4-ha area closed only to livestock since 1932 (hereafter, “protected plot”).

Percent cover and *P. velutina* plant density were tabulated within contiguous 20-m X 20-m subplots following protocols of (Glendening, 1952). Aboveground *P. velutina*

woody biomass was determined from field data using an allometric algorithm for canopy area (Archer unpublished data; see Browning et al. 2008). Patterns were evaluated with spatial autocorrelation structure of plant density. The land use history available for the SRER indicated the area had been treated with an aerial herbicide in 1965/1966, which confounds temporal evaluations; yet the grazing contrast remained intact.

In 1932, *P. velutina* cover and density was comparable on grazed and recently protected sites. By 1948, *P. velutina* cover on both plots had increased to comparable levels of cover, but plant densities on protected sites increased from 173 to 318 plants ha⁻¹ and those on grazed sites increased from 205 to 603 plants ha⁻¹, reflecting greater recruitment of new plants on the protected plot ($n = 205$) relative to grazed plot ($n = 62$). Application of an aerial herbicide in 1965/1966 reset cover across the entire study area. By 2006, *P. velutina* had rebounded, with cover and density on the protected area significantly exceeding that on the grazed area. However, total aboveground *P. velutina* biomass was comparable on grazed and protected plots by 2006 (2.1-Mg ha⁻¹).

Spatial metrics were more sensitive to the effects of livestock grazing than were estimates of percent cover. Patterns in spatial autocorrelation in plant density did not deviate from random over 74 years on the grazed plot, whereas patterns on the protected area became increasingly positive. Protection from livestock facilitated the formation of dense shrub clusters and shrub-free areas to produce high spatial heterogeneity. Collectively, the results suggest widespread generalizations that livestock grazing promotes woody plant encroachment are not robust. Indeed, in this semi-desert grassland ecosystem, livestock grazing retarded rather than promoted woody encroachment over 74

years. Results from this long-term study are in accordance with short-term seedling establishment studies with leguminous shrubs in other systems and indirectly point to the critical role of fire as a proximate factor regulating shrub establishment and stand development in grasslands.

Future Work

Two research interests will guide the next steps in my scientific career although I remain open to seizing new opportunities that may arise. I strive to understand how species are distributed across heterogeneous landscapes, how distributions change, and the ecological mechanisms associated with changes over time. In addition, I am thoroughly interested in applying tools from fields of spatial statistics, remote sensing, and geographic information science to natural resource problem solving. My dissertation was an attempt to understand the role of drivers in the change in woody plant abundance in rangelands. There is much yet to be done to disentangle the relative contributions of climate, elevation, landform, and land use history (e.g., livestock grazing and brush management). Future research directions are briefly outlined below:

Examining the roles of land form and climate on woody plant dynamics

The relative roles of land management (e.g., livestock grazing, fire suppression, and brush management) and climate in woody plant encroachment are controversial and may be mediated by elevation, soil properties, and landform (Archer 1995). I want to build on insights and experiences from studies in Appendices A and C to expand my time series analysis to include additional sites to explore the roles of landform (i.e., ephemeral

drainages and adjacent upland landscapes), elevation as a proxy for climate (mean annual precipitation), and brush management in woody stand recovery.

Point pattern analysis to examine spatial patterns of *P. velutina* recruitment processes for contrasting livestock grazing histories

This work would build on the findings from Appendix C and expand the understanding whether/how plant size influences *P. velutina* establishment patterns. Is recruitment more likely under or away from adult canopies? Might point-based spatial statistics reveal biotic interactions across a range of distances that might not be discernable using field-based measures conducted at fixed distances (i.e., Moran's I)? Answers to these questions could shed light on the role of competitive interactions in regulating shrub cover, density, and biomass to improve dynamic forecast modeling.

A multi-sensor, bottom up approach to assessing land cover characteristics in southwestern U.S. rangelands

There is widespread interest in understanding how land surface characteristics are translated across spatial scales in remote sensing. I have a keen interest in formulating a hierarchical approach that incorporates fine-scale, field based (i.e. bottom-up) perspectives with broad-scale, remotely-sensed (e.g., top-down) approaches for estimating percent cover, and biomass. A cross-scale, hierarchical framework using remotely sensed data from a range of sensor platforms is best suited for exploring scaling relationships of land surface characteristics important to land cover change and rangeland monitoring.

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APPENDIX A**WOODY PLANTS IN GRASSLANDS: POST-ENCROACHMENT DYNAMICS**

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Abstract:

Woody plant abundance is widely recognized to have increased in savannas and grasslands worldwide. The lack of information on the rates, dynamics and extent of increases in shrub abundance is a major source of uncertainty in assessing how this vegetation change has influenced biogeochemical cycles. Projecting future consequences of woody cover change on ecosystem function will require knowledge of where shrub cover in present-day stands lies relative to the realizable maximum for a given soil type within a bioclimatic region. We used time-series aerial photography (1936, 1966, and 1996) and field studies to quantify cover and biomass of velvet mesquite (*Prosopis velutina* Woot.) following its proliferation in a semi-desert grassland of Arizona. Mapping of individual shrubs indicated an encroachment phase characterized by high rates of bare patch colonization. Upon entering a stabilization phase, shrub cover increases associated with recruitment and canopy expansion were largely offset by contractions in canopy area of other shrub patches. Instances of shrub disappearance coincided with a period of below-average rainfall (1936 to 1966). Overall, mean (\pm SE) shrub cover on sandy uplands with few and widely scattered shrubs in 1902 was dynamically stable over the 1936 to 1996 period averaging ca. 35 (\pm 5)%. Shrub cover on clayey uplands in 1936 was 17 (\pm 2)%, but subsequently increased 2-fold to levels comparable to those on sandy uplands by 1966 (36 \pm 7%). Cover on both soils then decreased slightly between 1966 and 1996 to 28 (\pm 3)%. Thus, soil properties influenced the rate at which landscapes reached a dynamic equilibrium, but not the apparent endpoint. Although sandy and clayey landscapes appear to have stabilized at comparable

levels of cover, shrub biomass was 1.4-times greater on clayey soils. Declines in shrub cover between 1966 and 1996 were accompanied by a shift to smaller patch sizes on both sandy and clayey landscapes. Dynamics observed during the stabilization phase suggest density-dependent regulation may be in play. If woody cover has transitioned from directional increases to a dynamic equilibrium, biomass projections will require monitoring and modeling patch dynamics and stand structure rather than simply changes in total cover.

Key words: Santa Rita Experimental Range, shrub encroachment, *Prosopis velutina*, aerial photography, woody biomass, dynamic equilibrium, edaphic constraints, encroachment phase, stabilization phase, shifting mosaic

Introduction

Grasslands and savannas occupy ca. 40% of the land surface (Bailey 1996) and contribute 30-35% of the terrestrial net primary productivity (Field et al. 1998). As such, they play an important role in global carbon, water, and nitrogen cycles. Changes in land cover and land use are predominant drivers of global change (Vitousek 1992, 1994, Pielke et al. 2002). One of the most striking land cover changes in grasslands and savannas over the past 150 years has been the proliferation of trees and shrubs at the expense of perennial grasses. Although this shift in plant life-form composition has been widely reported (reviewed by Archer 1994 and Van Auken 2000), relatively little is known of the rates and dynamics of woody plant cover change and the consequences for ecosystem biogeochemistry. What is known is controversial and few robust generalizations have emerged (House et al. 2003, Wessman et al. 2004).

Woody plant encroachment has a potentially important, but poorly documented impact on the terrestrial carbon cycle (Houghton et al. 1999, Pacala et al. 2001, Houghton 2003a). Quantifying the magnitude of carbon sequestration accompanying changes in woody plant abundance in drylands is an important factor in landscape- and regional-scale assessments of aboveground carbon pools with strong links to soil organic carbon. Carbon uptake and biomass accumulation may be maximal in developing stands and plateau in mature stands (Hurt et al. 2002). Knowledge of stand age-structure is thus critical for forecasting ecosystem carbon sequestration potential. Given that woody plant encroachment in grasslands and savannas has been ongoing since the mid- to late 1800s (Archer et al. 1988, Archer 1995), it stands to reason that some, and perhaps many,

landscapes may be at or approaching maximum levels of cover, density or basal area; and hence maximum stand-level biomass. Determining the extent to which ecosystems may be approaching aboveground carbon sink saturation has important implications for land management and carbon trading markets (e.g., Burrows et al. 2002). What is the maximum shrub cover/density/biomass that might occur within a given bioclimatic region? The answer likely depends on soils and topography.

Soil properties (i.e., texture, depth, and fertility) and topography interact to influence patterns of woody plant abundance and distribution (Johnson and Tothill 1985, McAuliffe 1994). Combined, these factors determine how surface water, a critical resource in drylands, is distributed and utilized (Noy-Meir 1973, Tongway et al. 2001, Wilcox et al. 2003). Soil texture regulates the infiltration and percolation of rainfall, resulting in differential access to subsurface water based on life-form rooting patterns [e.g., deeply rooted shrubs versus shallow rooted grasses (Jackson et al. 1996)]. Generally, coarse-textured soils are thought to favor shrubs and finer-textured soils to favor grasses (Walker 1987, Scholes and Archer 1997). Topography-mediated patterns of run-off/run-on can override or reinforce texture constraints on woody plant distribution, such that woodlands can develop on fine-textured soils that might otherwise be expected to support grassland and open savanna (e.g., Wu and Archer 2005). Patterns of change in woody plant cover and carbon stocks observed using remotely sensed imagery have been related to soil types (Archer 1995, Hudak and Wessman 1998, Asner et al. 2003); and recent studies have illustrated how soil properties may influence grassland/shrubland ecotone dynamics (Bestelmeyer et al. 2006) and aboveground

primary production subsequent to shrub encroachment (Hughes et al. 2006). However the influence of soil properties on woody plant stand structure, dynamics, and stand development are not well known. Within a bioclimatic region, contrasting topo-edaphic landscape elements would be expected to differ in their susceptibility to woody plant encroachment and in their woody plant ‘carrying capacity.’ Shrub encroachment within a bioclimatic region may also depend on the seasonality of annual rainfall, with summer rainfall favoring grasses and winter rainfall favoring shrubs (Scholes and Walker 1993, Scholes and Archer 1997). Along these lines, it has been suggested that years of relatively high winter rainfall in the late 1970s triggered large increases in shrub densities in the Southwestern USA (Brown et al. 1997).

Shrubs in the genus *Prosopis* have proliferated over much of the Southwestern USA and in arid and semi-arid regions of Africa (e.g., MacDonald 1989), India (Sharma and Dakshini 1991), South America (Cabral et al. 2003) and Australia (e.g., van Klinken and Campbell 2001). Changes in velvet mesquite (*Prosopis velutina* Woot.) cover in desert grasslands on the Santa Rita Experimental Range (SRER) in southeastern Arizona have been particularly well-chronicled (e.g., Fig. 1 and McClaran 2003). Small (< 1-m tall) *P. velutina* plants were first observed in 1902 (Griffiths 1904), and Wooten (1916) qualitatively noted an increase in their stature and abundance by 1915. Glendening (1952), working on the SRER on plots established in 1932 and re-inventoried in 1948-9, found that cover increased on areas with < 30% canopy cover and decreased on areas with > 30% canopy cover. Based on these observations, he proposed woody cover would

stabilize at approximately 30%. How accurate is this prediction? How well does it hold up over larger spatial scales and contrasting soil types?

Our objective was to quantify landscape-scale changes in stand structure, cover and patch dynamics of *P. velutina* on contrasting interfluvial (hereafter “uplands”) soils in desert grasslands of southeastern Arizona. A time-series of aerial photography (1936, 1966, and 1996) was used to (i) quantify rates and dynamics of cover change on two distinct geomorphic surfaces; (ii) relate patterns of woody cover change to rainfall seasonality and test the hypothesis that shrub cover increases will follow years of relatively high winter precipitation (e.g., Brown et al., 1997); (iii) test the hypothesis that the rate and extent of *P. velutina* encroachment would be highest on coarse-textured soils and lowest on fine-textured soils; and (iv) evaluate Glendening’s (1952) prediction that *P. velutina* cover would stabilize at 30%. Furthermore, we sought to use allometric equations relating *P. velutina* canopy cover to biomass in conjunction with canopy cover estimates derived from aerial photographs to quantify changes in aboveground carbon mass accompanying woody plant encroachment. To assess the accuracy of using aerial photography to estimate shrub biomass on landscapes, we used field data to quantify how much woody plant biomass we might be missing; and how long it takes *P. velutina* plants to reach sizes discernable on aerial photography.

Methods

Study site

The study was conducted on the 21,514-ha Santa Rita Experimental Range (SRER) 45-km south of Tucson, Arizona (31° 49' 58" N, 110° 52' 24" W) along the western edge of the semi-desert grassland region of the Sonoran Desert (Brown 1994). Annual precipitation is bimodal with a pronounced peak in late summer (July-September monsoon) and a lesser peak in winter; mean annual precipitation is positively associated with elevation, ranging from 296-mm at lower elevations (866-m) to 498-mm at upper elevations (1372-m). Physiognomy ranges from *Larrea tridentata* desert scrub at the lowest elevations to *Quercus* spp. woodlands at the highest. *Prosopis velutina* is the dominant shrub at 990 – 1200-m elevation; other shrub species in this zone include *Celtis pallida* Torr., *Acacia greggii* Gray and the sub-shrub *Isocoma tenuisecta* Greene (the latter is not likely detected with image processing protocols employed) (McClaran 2003).

To quantify the extent to which soils influence the rate and extent of shrub cover change and to minimize potential confounding effects of livestock grazing, fire and precipitation, we confined our analyses to landscapes with similar land use history, topography and elevation. Sites meeting these criteria were identified on replicated, nearly level landscapes in the *P. velutina* vegetation zone at ca. 1,100-m elevation within Pasture 2S, a 557-ha management unit encompassing an area with no known history of fire or brush management. Changes in shrub cover were assessed using aerial photography from 1936, 1966, and 1996.

Precipitation, grazing and upland soils

Mean annual precipitation (1922-2002; derived from four gauges between 1,100 and 1,200-m elevation and within 4-km radius of our study area) was 370-mm with an average summer (June – September) precipitation of 213-mm (Coefficient of Variation, CV = 0.3) and an average winter precipitation (October – May) of 158-mm (CV = 0.4) (McClaran 2003). In the fourteen years prior to 1936, 43% of winters and 43% of summers experienced below-average rainfall (Figs. 3A & B). The period 1936 to 1966 was characterized by drier-than-average winters (70% of years), with 23% of years receiving below-average precipitation for the entire rain year (Oct-Sep) (Fig. 3C). In contrast, 1966 to 1996 was a relatively high rainfall period marked by extremely wet summers in 1984 and 1990; and few years of below-average annual rainfall (Fig. 3C). Winter rainfall from 1966 to 1996 was generally above-average (57% of years), with the thirteen consecutive winters preceding the 1996 image date exhibiting above-average winter rainfall.

Prior to establishment of the SRER in 1903, the area was subjected to heavy, year-long, unregulated cattle grazing. Shortly after establishment of the SRER, cattle were removed and re-introduced in 1916. Since that time, stocking rates and seasonal livestock use have varied (e.g., Pasture 2S, Fig. 3D). Year-long grazing was practiced from 1916 until 1972 with steadily decreasing stocking rates from a maximum of 0.174 animal unit years per ha in 1918. A rotational grazing system (Martin and Severson 1988) was implemented in 1972 and maintained through the 1996 image date.

Shrub cover was quantified on eight landscapes within a 200-ha portion of Pasture 2S. Soils on the SRER were mapped on the basis of age, texture, and depth as a third-order soil survey (Breckenfeld and Robinette 1997). Sampling was confined to areas classified as either the Holocene-age Combate-Diaspar complex or the late Pleistocene-age Sasabe-Baboquivari complex based on criteria described in Batchily et al. (2003); soil inclusions composed 10 to 15% of each soil complex (Breckenfeld and Robinette 1997). The Combate-Diaspar soils were Entisols (coarse-loamy, mixed, superactive, nonacid, thermic Ustic Torrifuvents). Soil profile development was minimal; the dominant subsurface texture for Combate soils was coarse sandy loam. Average (\pm SE) maximum clay content was $16.8 \pm 1.1\%$ at a mean depth of 33 ± 8.5 -cm [from trenches characterized by Batchily et al. (2003)]. The Sasabe-Baboquivari soils were Aridisols (fine, mixed, superactive, thermic Ustic Paleargids) with accumulations of clay at an average depth of 23.4 ± 5.1 -cm and an average maximum clay content of $24.9 \pm 1.8\%$ (Batchily et al. 2003). The dominant subsurface texture for Sasabe soils was sandy clay loam. For expediency, we will subsequently refer to these soil complexes by the contrasting sub-surface textures: “sandy” for the Combate-Diaspar complex and “clayey” for the Sasabe-Baboquivari complex.

Arroyos and ephemeral drainages dissect the extensive alluvial fan terrace where the study was conducted, generating topo-edaphic heterogeneity. To standardize for this heterogeneity, we confined sampling to the nearly level uplands separating arroyos and drainages. Uplands were mapped within a Geographic Information System (GIS) [ArcGIS v.9.0, (Environmental Science Research Institute Inc. 2004)] by digitizing

drainage channels on aerial photography and applying a 30-m buffer. Drainages and their buffer zones were excluded from cover change analysis. The resulting eight soil map polygons were buffered 70-m to minimize the likelihood of sampling in edaphic ecotones. Partitioning within the 200-ha area in this manner resulted in three “sandy” and five “clayey” landscapes that ranged from 1.0 to 7.2-ha in size.

Aerial photography

Aerial photo dates included February 1936 (scale 1:31,640, black/white), August 1966 (1:15,640, black/white), and June 1996 (1:40,000, color-infrared [CIR]). June 1996 photos were acquired as Digital Ortho-Quarter Quadrangles (DOQQ) from the U.S. Geological Survey. Film negatives for 1936 and 1966 imagery were scanned at 1200 dpi, geometrically-corrected to the 1996 ortho-rectified base image with a root mean-square error of < 1 pixel (or 1-m), and resampled to a common spatial resolution (1-m) using ERDAS Imagine™, Version 8.7 (ERDAS Inc. 2002). The sample unit in our analysis was a shrub patch, defined as a woody plant canopy that could represent an individual plant or a cluster of plants with touching or overlapping canopies.

Automated image classification protocols were used to delineate shrub patches in geo-coded, ortho-rectified images. To remedy issues related to differences in photo scale, we resampled all images to a common spatial resolution (1-m). Shrub patches in the 1936 and 1966 images were delineated using a supervised classification applied to the panchromatic band and a texture layer (Asner et al. 2003). Red, green, and near-infrared image bands were used in the supervised classification of the 1996 CIR image. Texture served as a contrast index within a designated focal window passed across the image

(Nellis and Briggs 1989, Anys et al. 1994). For this application, the texture layer distinguished dark shrub canopies from the surrounding bright soil or herbaceous vegetation. Texture was calculated as the variance within a 3 x 3 pixel (0.6-m pixel size, 3.25-m²) window prior to re-sampling 1936 and 1966 images. Effort was made to maintain consistency with bands used to classify images, but incorporating the texture layer with the 1996 image bands over-estimated the size of woody plant canopies. Therefore, we used the color and near-infrared bands, which outperformed other band combinations to classify 1996 woody plant cover.

Supervised classification algorithms require derivation of signatures to represent all land cover classes contained in the image. Due to the differences in information content between panchromatic and CIR photography, we were able to extract grass cover, bare ground, and shrub canopy classes from the 1996 image while only reliably distinguishing shrub canopy from non-shrub classes in the 1936 and 1966 black and white photographs. Shadow can induce errors in vegetation cover estimates from panchromatic aerial photography (Whiteman and Brown 1998). We were unable to explicitly account for shadow effects with limited metadata for historic imagery. We recognize that shadow effects may have exaggerated perceived shrub patch canopy area; however, this potential error was minimized due to the flat terrain (circumventing topographic effects) and by using photo subsets from the center of the image (thus avoiding vignetting along edges). To alleviate the salt-and-pepper appearance of the output classified images, which commonly results from supervised classification algorithms applied on a pixel-by-pixel basis, a majority filter was applied to eliminate all

patches comprising fewer than 4 pixels (Lillesand and Kiefer 2000). Therefore the smallest discernible shrub patch in the classified aerial photography was 4-m² in size.

Classification accuracies were assessed using a random sample of points stratified by image class. Random points on photographic images were assigned manually to the reference class ‘shrub’ or ‘non-shrub’ for 1936 and 1966 images ($n = 100$) and ‘grass,’ ‘shrub,’ or ‘bare ground’ for the 1996 image ($n = 150$). Classification accuracies represent the level of agreement between manual and automated image class assignments and are presented as error matrices along with Cohen’s Kappa (K^{\wedge}) Statistic, an estimate of accuracy that incorporates agreement that may occur by chance (Cohen 1960, Congalton and Green 1999). Values of Kappa range from 0 to 1.0; values > 0.75 indicate strong agreement beyond chance; values < 0.40 reflect poor agreement.

To estimate the time required for woody plants to attain canopy sizes distinguishable on aerial photography, we made use of field canopy measurements made in 1932 and 1948 and stored in the SRER data archives (summarized in Glendening 1952). These data included canopy diameter measurements for all *P. velutina* trees in plots 200-m from our study site on clayey soils. From this database, we extracted canopy dimensions for *P. velutina* plants present in 1948 but absent in 1932. Thus, the maximum age of selected trees would be 16-y. We plotted the size-class distribution of these trees and used the 95th percentile as a break point to identify trees most likely to have established soon after the 1932 census. Canopy growth rates of these trees (m²/y; $n = 8$) were estimated by dividing canopy area in 1948 by 16-y.

Shrub cover

Shrub cover (%) on each landscape was determined by dividing the number of cells (i.e., pixels in classified photography) mapped as 'shrub' by total number of cells in each landscape. Diagnostic procedures were applied to shrub cover data prior to analysis and studentized residuals (R student) were used to detect outliers. Repeated measures analysis of variance (ANOVA) was used to assess whether changes in shrub cover on the sandy and clayey soils differed from each other over time. Mauchly's sphericity test was used to examine the form of the common covariance matrix and to ascertain whether univariate or multivariate interpretations were appropriate (SAS Institute 2002). Mauchly's criterion for sphericity was not violated; therefore univariate results for repeated measures ANOVA are reported.

Patch dynamics, structure and biomass

Shrub patch dynamics were analyzed with a two-tier approach utilizing patch size distributions generated from the automated classification in conjunction with manually delineated shrub patches randomly selected within each landscape. Shrub patch size derived from aerial photos was determined using cell (i.e., pixel) counts to represent patch area. Individual patches were defined by cell adjacency using an 8-neighbor rule. Statistical differences in patch size distributions by date and by soil type were assessed using Kolmogorov-Smirnoff two-sample tests (Daniel 1978). Patches intersecting pre-defined study site boundaries were withheld from computations of size distributions.

To capture finer-scale patch dynamics (e.g., fragmentation of large patches, appearance of new patches, and coalescence of neighboring patches), we monitored a

subset of individual shrub and non-shrub patches through time. In each landscape, we randomly selected 5 to 14 shrub patches spanning the range of sizes present on the 1936 aerial photography (to minimize potential bias, the number of patches selected was weighted by landscape area). Canopies of selected shrub patches were hand-digitized and changes in individual patch area were categorized as: (1) no change (change in patch area < 15%), (2) growth by canopy expansion, (3) growth by coalescence with neighboring patches, (4) loss by canopy die-back (decrease in area without fragmentation into separate patches), (5) loss by fragmentation (decrease in area accompanied by creation of multiple small patches from a single larger patch), or (6) patch disappearance.

We also identified 11 to 17 circular 50-m² patches not occupied by shrubs (hereafter “non-shrub patches”) on each landscape on the 1936 photo to monitor shrub recruitment and development in the 1966 and 1996 imagery. When shrubs subsequently occupied non-shrub patches, the occurrence was categorized as: (1) establishment, (2) encroachment by a neighboring shrub patch, or (3) both. The probability of non-shrub patches being colonized by shrub patches was calculated and χ^2 analysis was used to test whether shrub colonization rates were affected by date or soil type.

Patch structure on contrasting soils was evaluated by measuring canopy dimensions of all shrub patches in 30 x 30-m field plots ($n = 5$ on sandy soils; $n = 3$ on clayey soils) in 2004. Based on a preliminary study, patch canopy area was computed as a circle whose diameter was the average of the longest axis and its perpendicular bisector. On aerial photos, plants with contiguous or overlapping canopies appear as a single patch; thus, we also measured all shrubs whose canopies touched or overlapped as a

single patch and recorded the number of individuals comprising the patch. Natural breaks in the size-class distributions were used to delineate patch size classes. We tested for differences in the patch size, patch density, and number of individuals/patch between soils using ANOVA.

Total aboveground *P. velutina* biomass was nondestructively estimated using a regression equation developed for plants at our site: $\ln TB = 1.6 * \ln CA - 0.58$ ($R^2 = 0.97$, $F = 807.5$, $df = 1, 29$, *unpublished data*), where TB is total biomass [kg of dry leaves + wood] and CA is the field-measured canopy area (m^2). *P. velutina* biomass density was then estimated from measurements of the canopies of all plants (or patches, in cases where plant canopies intersected) in eight 30 x 30-m plots. These field-based biomass assessments were then used to quantify biomass missed with remotely sensed data and determine the relative contribution of various patch size-classes to whole-plot aboveground woody biomass. Carbon mass was estimated by multiplying *P. velutina* biomass by 0.47 (a site-specific conversion that takes into account the relative contribution of leaf, twig, branch and trunk tissues to total aboveground mass; *unpublished data*).

Results

Field Assessments

Shrub cover in field plots was 99% *P. velutina*. Field measurements in 2004 revealed differences in the number of plants/patch ($F = 6.04$, $df = 1, 270$, $p = 0.015$), patch size ($F = 10.62$, $df = 1, 270$, $p = 0.001$), and patch size-class distributions ($KS_a = 1.654$, $p = 0.008$) on sandy and clayey surfaces (Figs. 4A and B). *P. velutina* patches on

sandy sites were less numerous, but larger than those on clayey sites with fewer plants/patch; and patch sizes were more strongly skewed toward smaller classes on clayey soils compared to sandy soils. On sandy soils, 45% of patches were below the detection limit on aerial photos ($< 4\text{-m}^2$), compared to 64% on clayey soils. Patches $< 5\text{-m}^2$ canopy area constituted 1.9% and 6.5% of the aboveground *P. velutina* biomass/carbon mass on sandy and clayey sites, respectively (Fig. 4C). Carbon mass associated with *P. velutina* in plots on clayey sites was 1.4 times greater than that on sandy sites (Fig. 4C). The largest contribution to overall carbon mass on both soils was from patches in intermediate size classes (11 to 25 and 26 to 50- m^2).

Empirical evidence for rates of *P. velutina* canopy growth was generated from 1932 and 1948 field measurements. Mean (SE) canopy size of the eight largest plants measured in 1948 and deemed to have established circa 1932 was $3.95 (0.22)\text{-m}^2$ (range = 3.18 to 4.67-m^2) representing an average 16-y growth rate of $0.25 (0.01)\text{ m}^2\text{ y}^{-1}$ (range = 0.20 to $0.29\text{ m}^2\text{ y}^{-1}$).

Image classification accuracy

Automated image classifications yielded satisfactory measures of shrub canopy cover as determined by Cohen's Kappa statistics (0.75, 0.68, and 1.00 for 1936, 1966, and 1996 images, respectively) and image classification accuracies derived from the error matrices (Table 1). Image quality was consistent across the study site within each image. Small differences in the ability to distinguish shrubs from the surrounding bare ground or grassy matrix between image dates were evident from the Kappa statistics. Shrub canopy boundaries were somewhat less distinct in the 1966 image when re-sampled to common

spatial resolution (1-m). Producer's accuracies for the shrub canopy class representing the probability of correctly classifying canopies from surrounding bare ground or grass were high (> 84%) for all image dates.

Changes in shrub cover and patch size distributions

An inherent limitation of aerial photography is the inability to confidently distinguish individuals. The high degree of shrub aggregation on our study sites necessitated delineation of patches rather than individuals and hence precluded the use of individual plant-based algorithms for estimating biomass. Automated image classification, which allowed broad spatial coverage, was not able to reliably distinguish between single- and multi-plant patches or to determine the number and size of individual canopies in multi-plant patches on the aerial photos available to us (Fig. 5). Thus, we could not use the imagery to quantify the size-class distributions of individual *P. velutina* plants. Furthermore, because our cover-biomass algorithms were based on individual plant measurements, we could not use them to estimate *P. velutina* aboveground biomass from aerial photos.

Mean (CV) shrub cover on 1936 aerial photos was 35% (0.2) on sandy soils and 22% (0.6) on clayey soils. One clayey landscape was an extreme statistical outlier (R Student = 3.93). Shrub cover on this precocious clayey landscape was exceptionally high in 1936 (44%) in comparison to all other landscapes on clayey soils (< 20%). Removal of the outlier clayey landscape from the repeated measures ANOVA revealed a strong soil type X date interaction ($F = 6.27$, $df = 2, 10$, $p = 0.017$) that was otherwise masked ($F = 2.94$, $df = 2, 12$, $p = 0.0914$) (Fig. 6). Field surveys and a review of SRER records

failed to reveal any differences in spatial context, land use, disturbance history, soils or topography that might have caused this site to have such high shrub cover in 1936.

Summaries that follow exclude the discordant clayey landscape.

Patch density on the two soil types was comparable on the 1936 aerial photos (Fig. 6B), but mean shrub cover was considerably higher on sandy soils (37%) than clayey soils (17%) (Fig. 6A). This cover-density dichotomy was the result of larger shrub patches on the sandy surfaces (Table 2). By 1966, cover was comparable on sandy and clayey landscapes (34 and 36%, respectively), owing to slight declines on sandy soils and a 2-fold increase on clayey soils. Shrub cover on both sandy and clayey surfaces then decreased between 1966 and 1996 (to 27 and 28%, respectively).

The 113% increase in shrub cover on clayey landscapes between 1936 and 1966 was accompanied by an increase in patch density (from 38 to 48 patches ha^{-1}) (Fig. 6B). In contrast, cover remained stable on sandy surfaces at 35%, while patch density decreased from 39 to 33 patches ha^{-1} . Patch size distributions on the two soil surfaces in 1936 ($\text{KS}_a = 2.937$, $p < 0.0001$) and 1966 ($\text{KS}_a = 2.465$, $p < 0.0001$) were significantly different. Sandy landscapes were characterized by fewer, but larger patches than clayey landscapes (Fig. 6B, Table 2). Increases in patch density between 1966 and 1996 (from 33 to 53 and from 48 to 69 patches ha^{-1} for sandy and clayey sites, respectively) were accompanied by decreases in cover (Figs. 6A, B). By 1996, patch size distributions were similar on both soils ($\text{KS}_a = 1.329$, $p = 0.059$). Temporal comparisons of patch size distributions revealed a statistically significant shift to a greater proportion of small patches between 1966 and 1996 on both soils (sandy $\text{KS}_a = 2.686$, $p < 0.0001$; clayey KS_a

= 1.804, $p = 0.0030$) with a 2-fold increase in the number of patches in the smallest size classes on both soils.

Patch dynamics

Half (50%) of the individual shrub patches tracked on sandy soils ($n = 28$) declined in canopy area between 1936 and 1966, whereas 71% of the shrub patches on clayey soils ($n = 35$) maintained or increased their canopy area (Fig. 7A). From 1966-1996, a period of landscape-scale declines in total shrub cover (Fig. 6A), the majority of individual shrub patches on both soil types (72 and 68%) declined in area (Fig. 7B). Four shrub patches disappeared between 1936 and 1966 (3 on sandy and 1 on clayey soils); no losses were observed in the 1966 to 1996 period.

The proportion of 50-m² shrub-free patches in 1936 that contained shrubs in 1966 was significantly higher on clayey surfaces than sandy surfaces (55 vs. 23%; $\chi^2 = 11.1$, $df = 1$, $p = 0.001$) (Fig. 8A). Cumulative counts in 1996 revealed that clayey surfaces maintained a significantly higher proportion of colonized patches ($\chi^2 = 4.4$, $df = 1$, $p = 0.035$). On sandy sites, recruitment of shrubs into shrub-free areas was similar in both 1936 – 1966 (23% of shrub-free patches) and 1966 – 1996 (24% of shrub-free patches). In contrast, recruitment on clayey sites decreased dramatically from 54% of shrub-free patches between 1936 and 1966 to 20% between 1966 and 1996. When woody plant colonization was evaluated by period and soil type (i.e., new recruits in each time period), there was no statistically significant difference on the two soils from 1966 – 1996 ($\chi^2 = 0.002$, $df = 1$, $p = 0.967$) (Fig. 8B). Shrub occupation of previously non-shrub patches was primarily via recruitment rather than expansion of nearby shrub canopies.

Discussion

Woody plant abundance has increased in savannas and grasslands worldwide with potentially important (Pacala et al. 2001, Houghton 2003b), but as yet poorly quantified implications for the carbon, nitrogen and water cycles (Archer et al. 2001, Huxman et al. 2005). Changes in fractional woody plant cover correspond to changes in aboveground carbon (C) pools; changes in aboveground C pools are often accompanied by lagged changes in belowground C pools (Hibbard et al. 2003). Although woody cover appears to have peaked and stabilized on the desert grassland site in this study (see also McClaran and Angell 2006), soil organic carbon accumulation rates are still on a positive trajectory (Wheeler et al. 2007). Forecasting future changes in above- and belowground C pools will require resolution of uncertainties involving interactions among climate, soils, atmospheric CO₂ enrichment and disturbance. This study capitalized on the long-term, large-scale synoptic perspectives provided with historical aerial photography to quantify changes in woody plant cover over 60 years, while minimizing the potentially confounding effects of climate, topography, land use (livestock grazing and fire history), elevation, and shrub species.

Aerial photography and woody plant biomass

Remote sensing operations afford comprehensive and repeatable assessments of land cover change at broad spatial scales and yield a suite of tools for mapping and monitoring changes in vegetation cover (Asner et al. 2003, Okin and Roberts 2004, Okin 2007). As such, remote sensing plays an increasingly prominent role in estimating terrestrial plant biomass (reviewed by Lu 2006). Quantifying land cover classification

accuracy and uncertainty associated with estimates of plant biomass is paramount (Foody 2002). One important, yet outstanding challenge associated with estimating biomass from remotely sensed imagery is to appropriately link field data to remotely sensed estimates of aboveground biomass (Lu 2006). Aerial photography provides opportunities to quantify woody patch dynamics and stand structure as a link to coarse resolution satellite imagery for improving accuracy of terrestrial biomass and carbon storage estimates. However, in our case, the inability to distinguish individual shrub canopies on aerial photos was a major limitation for quantifying plant population structure and biomass. We undertook this study intending to estimate shrub aboveground carbon mass at landscape scales using plant canopy area-biomass relationships developed in field studies. Unfortunately, the occurrence of multiple-plant shrub patches, aerial photo detection limits, and use of automated classification algorithms prevented delineation of individual shrub canopies. In this system, *P. velutina* biomass increases exponentially with canopy area (data not shown). Applying the non-linear canopy area-biomass relationships derived for individual plants may therefore substantially over-estimate biomass in cases where conglomerates of individual shrubs were treated as a single plant with a large canopy area. Indeed, many of the classified patches had canopy areas far beyond those of the largest *P. velutina* plants on the landscape (Table 3), and hence well beyond the range of data used to construct canopy area-biomass regressions. Manual classification may alleviate these problems with enhanced perception of individual plant canopies. However, there would be important trade-offs: observer-to-observer subjectivity, bias, and criteria for defining ‘a shrub’ (e.g., Fensham and Fairfax 2007);

and manual classifications could not be feasibly applied over large areas. In lieu of higher quality, higher resolution photographic imagery, one could develop canopy area-biomass algorithms at the scale of the patches that can be readily distinguished on the aerial photography.

Overestimates of aboveground biomass would be partially offset by failing to account for shrubs whose canopy areas are below detection limits on aerial photography. For the scale/quality of aerial photos available for this Sonoran Desert mesquite shrubland, we estimated that 6% of the shrub aboveground biomass on the landscape was associated with patches smaller than the minimum mapping unit (4-m²). The extent of under-estimation would increase with increases in pixel size (i.e., spatial resolution) and with declines in image quality (Table 4). Although small shrubs comprised a relatively small fraction of the aboveground woody biomass, they represent a dynamic portion of the plant population with high growth potential and, presumably, the highest sensitivity to environmental stresses such as drought and fire. As such, detection limits of aerial photography constrain its utility in large-scale monitoring of woody plant population dynamics and in providing growth, and age structure parameters for biogeochemical models.

Seasonal precipitation and woody cover change

Shifts from summer to winter rainfall have been widely hypothesized as a mechanism driving woody plant increases in drylands (Hastings and Turner 1965, Archer 1994). Brown et al. (1997) used time-series aerial photography to document changes in woody plant density in Chihuahuan Desert communities and argued that the 3-fold

increases observed since the 1970s were the result of increased winter rainfall. Winter precipitation at our SRER site was also above-average for the 1970s and 1980s, and we too observed a 2-fold increase in the number small (4 to 5-m²) patches on both soils over this time frame ([inset histograms, Fig. 9](#)). Interestingly, this increase in patch density corresponded to a net decline in total woody cover. Field surveys in 2004 also revealed the existence of numerous small (< 1-m² canopy area) shrubs on both soils indicative of relatively recent recruitment of new plants. Based on our crude growth-rate estimates, such plants would have established in the late 1980s - early 1990s, an additional period of elevated winter precipitation.

Although there appears to be a loose correlation between increases in woody plant abundance on aerial photos and periods of increased winter precipitation, a cause-effect assertion is perhaps too simplistic for several reasons. First, when using time-series photography to relate approximate establishment dates to climatic factors, the time-lag between when a plant actually establishes and when it reaches a size that can be detected on a photo must be taken into account: ca. 16-y in our case. Thus, a 4-m² shrub on the 1996 image may have established ca. 1980. Hence the climatic conditions in and around this time would be most germane for plants of this size. It should be noted that this growth estimate is very crude and reflects canopy expansion over a relatively dry period on landscapes with low initial shrub cover. For larger (older) plants, estimates of recruitment dates are much more elusive; and would be subject to many more caveats. Second, little is known about factors regulating recruitment of dryland shrubs. Episodic recruitment in response to specific climatic triggering events has been widely reported

(e.g., Watson et al. 1997); and ‘snapshots’ widely spaced in time are not likely to capture these. Thus there is the real risk of spurious correlations when relating decadal patterns of change to patterns of annual and seasonal climate. Third, the increase in patch densities observed in our study also coincided with above-average summer rainfall and hence above-average annual rainfall. It could well be that the combination of elevated summer and winter rainfall was key to promoting recruitment. Fourth, although recruitment of new shrubs was observed during the 1966-1996 period, rates of recruitment were comparable (sandy sites) to 4.3 times higher (clayey sites), between 1936 and 1966, a period of erratic and relatively non-remarkable fluctuation in winter precipitation; and a period of relatively dry summers. Fifth, although shrub patch density increased during the relatively high rainfall 1966-1996 period, total cover actually declined. This decline in shrub cover encapsulated fragmentation of some pre-existing patches, contributing to elevated density estimates. These reductions in shrub cover during a relatively wet period may reflect that *P. velutina* stands have reached a stage where density-dependent interactions may be regulating how the community responds to precipitation. A better understanding of the relationship between shrub recruitment and climate is needed if we are to confidently forecast vegetation response to future environmental conditions.

Edaphic influences

Topoedaphic heterogeneity influences the rates and dynamics of plant response to climate and disturbance. We hypothesized that the rate and extent of woody plant proliferation on coarse-textured desert grasslands soils would be greater than those

occurring on finer-textured soils. Historic ground photography (ca. 1902) and earliest accounts of vegetation composition indicate *P. velutina* was largely absent from mid- to low-elevations uplands on the SRER at the turn of the century (Griffiths 1904, 1910). However, by the date of the first available aerial photography in 1936, shrub cover on sandy upland landscapes had reached ca. 35%, a peak value relative to the 1966 and 1996 photo dates. Thus, it appears that the physiognomic conversion of desert grassland to shrubland occurred during the 34 years preceding the 1936 aerial photography. With the exception of one landscape, woody cover changes on clayey soils (e.g., Fig. 1) lagged well behind those on sandy soils, such that the grassland-to-shrubland transformation took about twice as long (ca. 60-y) to occur. This is consistent with the general hypothesis that sandy soils should be more prone to woody plant encroachment than clayey soils. However, the fact that shrub communities developing on the two soil types have converged around a comparable mean cover was a surprise. Our data suggest that these desert grassland landscapes undergoing shrub proliferation transitioned from a period of directional change to one of dynamic fluctuation beginning in the 1930s (sandy sites) and 1960s (clayey sites). If this interpretation is correct, and barring climate change, future projections of woody cover and biomass will be determined more by patch dynamics than by net changes in fractional cover. Although total woody cover has reached a comparable level on these contrasting soils, it is not yet clear how differences in stand structure (inset histograms, Fig. 9) might dictate their future dynamics and response to climate fluctuation, climate change or disturbance.

At what point might the clay content of upland soils constitute a barrier to woody plant encroachment? Shrub cover appears to have stabilized at ca. 35% on Holocene- and late-Pleistocene-age surfaces with clay contents ranging from 16.8 to 24.9% respectively. However, other landscapes on the SRER characterized by soils of middle- (300,000 to 400,000 ybp) to early- (400,000 to 2,000,000 ybp) Pleistocene age (Batchily et al. 2003) with clay contents of 39% (from Fravolini et al. 2005) have resisted the shrub encroachment observed on other landscapes. These sites are characterized by grasslands with very little *P. velutina* cover (< 5 %) (McAuliffe 1995, McClaran 2003). Thus, a threshold clay content conferring resistance to shrub encroachment may lie somewhere between ca. 25 and 39% in this bioclimatic region.

What might the future hold for shrub encroachment on the early-Pleistocene surfaces currently dominated by grasslands? One possibility is that these older soils with their higher clay content will be resistant to shrub encroachment and the existing grassland physiognomy will be maintained indefinitely (Fig. 9, Scenario A). Alternatively, shrub encroachment on the early-Pleistocene surfaces may be lag behind that observed on late-Pleistocene surfaces similar to the lag observed on late-Pleistocene soils relative to Holocene soils (Fig. 9, Scenario B). The 'lag' scenario further begs the question 'At what level will woody cover on early-Pleistocene sites stabilize?' Recent and future changes in atmospheric CO₂ concentrations may favor shrubs over grasses (Morgan et al. 2007) and recent invasions of exotic grasses (McClaran and Anable 1992) may fundamentally alter fire regimes, thus complicating the extrapolation of past trends into the future. Resolution of these competing scenarios (Fig. 9 A and B) in the context

of projected climate change will be required if we are to project the future mix of herbaceous and woody vegetation in the region.

Although sandy and clayey landscapes appear to have stabilized at comparable levels of woody cover, they differ substantially in aboveground shrub biomass. Substantial differences in aboveground biomass in conjunction with the fact that development of shrub cover on clayey soils lagged well behind that on sandy soils, suggests edaphic influences change from the seedling to the post-establishment phase of the shrub life cycle. Our data suggest that conditions conducive to shrub seedling establishment and early persistence occur more frequently on sandy soils than on clayey soils; but that once established, the higher nutrient status and water holding capacity of clay soils ultimately enhances woody plant productivity and biomass accumulation (Scholes 1990). Differences in aboveground woody biomass reflected in size class structure on clayey and sandy soils may become more pronounced over time as small plants grow into larger size classes unless density-dependent regulation stabilizes woody biomass.

Woody cover dynamic equilibrium

The combined approach using patch and landscape perspectives to evaluate changes in woody plant cover over 60 years revealed patch-level fluctuations within the context of broad-scale stability. Based on field measurements of plant growth rates at the SRER site, Glendening (1952) predicted a maximum shrub cover of approximately 30%. Our time-series aerial photographic analyses generally support this prediction and further indicate that it appears to be robustly applicable on soils whose clay content and depth to

peak clay content ranged from 16.8 to 24.9% and 33- to 23-cm, respectively.

Furthermore, dynamic stabilization of shrub cover at ca. 30-35% in this Southwestern desert grassland is consistent with predictions of maximum cover that might be expected from an annual rainfall perspective. In a continental analysis of 854 sites, Sankaran et al. (2005) found that maximum woody cover in areas of Africa receiving less than 650 mm y^{-1} mean annual precipitation (MAP) was controlled by and increases linearly with MAP. Their data predict that our site with a MAP of 370-mm would have a maximum shrub cover of $\sim 37\%$. The concurrence of proposed regulatory mechanisms for African drylands and this North American system is promising and provides a framework for exploring how forecasted climate scenarios might influence future woody plant dynamics across large spatial scales.

Landscape-scale shrub cover dynamics reflect the net outcome of plant recruitment, plant canopy expansion and reduction, and mortality. Our data from a patch-perspective suggest each of these factors co-occur and wax and wane at decadal time-scales consistent with the shifting mosaic model of ecosystem development first identified for forests (Bormann and Likens 1979) and subsequently proposed for savannas (Scholes and Archer 1997). At our desert grassland site, cover increases associated with shrub recruitment and canopy expansion out-paced cover declines associated with canopy reductions and mortality during the ‘encroachment phase’ which continued until landscapes entered a ‘stabilization phase’ wherein recruitment and canopy expansion appear to decrease and were roughly offset by reductions in canopy area. Regulation of shrub cover in this stabilization phase may depend on the intensity of shrub-shrub

interactions and density-dependent regulation. The vast majority of species interactions research in savannas and grasslands invaded by woody plants has emphasized the effects of woody plants on herbaceous plants (House et al. 2003). The little that is known about intra- or interspecific interactions among woody plants and density-dependent regulation in shrublands and savannas has been largely inferred indirectly from pattern analyses (e.g., Duncan 1991, Martens et al. 1997, Scholes and Archer 1997). Removal experiments in shrublands have shown that the occurrence and intensity of shrub-shrub competition will vary with resource availability and rooting patterns (Manning and Barbour 1988, McPherson and Wright 1989, Scholes 1990). Experimental tests of shrub-shrub and tree-tree interactions in grasslands invaded by woody plants would be instructive next steps. Transitions from directional increases in woody cover in grassland and savanna systems to fluctuations around a dynamic equilibrium will necessitate re-evaluation of land management strategies and incorporation of patch dynamics into projections of change. Edaphic influences on changes in woody cover and biomass may be contingent on the stage of stand development and the nature of density-dependent interactions among shrubs. Once landscapes reach their woody cover 'carrying capacity,' predictions of future woody biomass and the rate and magnitude of plant and soil carbon storage will depend on quantifying shifts in population size structure rather than simple changes in net cover.

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Tables:

Table 1. Error matrices based on a random sample of points stratified by image class for 1936 ($n = 100$ points), 1966 ($n = 100$ points), and 1996 ($n = 150$ points) classified aerial photographs. User's accuracy represents the probability that a pixel classified on the map actually represents that category on the ground, while producer's accuracy represents the probability of a reference pixel (known) being correctly classified.

Classified Data	Reference Data				Accuracies (%)	
	Shrub Canopy	Non- Shrub	Grass Cover	Bare Ground	Producer's	User's
1936 Shrub canopy	34	5			87.2	85.0
Non-shrub	5	55			90.2	91.7
Reference Total	39	61			Overall 1936 = 89.0	
1966 Shrub canopy	32	6			84.2	80.0
Non-shrub	8	54			87.1	90.0
Reference Total	40	60			Overall 1966 = 86.0	
1996 Shrub canopy	47				94.0	100.0
Grass Cover	3		53	7	100.0	84.1
Bare Ground				40	85.1	100.0
Reference Total	50		53	47	Overall 1996 = 93.3	

Table 2. Descriptive attributes for shrub patch size distributions from 1936, 1966, and 1996 derived from automated classification of woody plant cover on aerial photography for sandy and clayey soil surfaces.

Patch attributes	Soil type					
	Sandy			Clayey		
	1936	1966	1996	1936	1966	1996
Mean size (m ²)	80.2	70.9	39.7	48.5	52.2	33.5
<i>n</i>	435	423	656	723	851	1327
C.V.	1.9	1.6	1.4	2.3	2.4	1.4
Median	37	33	17	23	20	18
Skewness	5.5	4.2	3.6	10.5	12.3	3.9

Table 3. Maximum patch size for woody plant cover derived from 1936, 1966, and 1996 aerial photography using a supervised classification algorithm. Patches less than 4 pixels (4 m^2) in size were dissolved. Aboveground biomass was derived using an allometric relationship relating canopy area to biomass.

Image Year	Maximum patch size (m^2)	Biomass (kg)
1936	2074	109,648
1966	2636	160,769
1996	530	12,426

Table 4. Percentage of aboveground woody biomass that would not be captured with aerial photography using different size thresholds from a field census of all *P. velutina* patches in eight 30 x 30-m plots on sandy ($n = 104$ patches) and clayey ($n = 168$ patches) soils on the Santa Rita Experimental Range in southeastern Arizona.

Detection Limit	Percent biomass missed	
	Sandy	Clayey
4 m ²	1.3	4.7
5 m ²	1.9	6.5
10 m ²	9.8	18.7
25 m ²	48.1	50.8
50 m ²	88.2	88.6

Figure Legends:

Fig. 1. Repeat ground photography (1922, 1962, and 2003) of vegetation change on a clayey soil site in a semi-desert grassland (Photo Station 111, Santa Rita Experimental Range digital photo archive; <http://ag.arizona.edu/SRER/photos.html>) at 1,100-m elevation (400-m from our study site). Arrows denote fixed-location rebar. (A) Shrub cover was low in 1922; (B) by 1962, velvet mesquite (*Prosopis velutina* Woot.), cholla (*Optuntia* spp.) and burroweed (*Isocoma tenuisecta* Greene) abundance had increased markedly; and (C) mesquite abundance remained high through 2003, while cholla and burroweed abundance declined.

Fig. 2. Location of the Santa Rita Experimental Range within the Sonoran Desert (depicted with gray on inset map) spanning the southwest United States and northwest Mexico (After Brown et al. 1998). Elevation is represented with 90-m contour lines and the extent of our study area is shown in gray.

Fig. 3. Seasonal precipitation and cattle stocking rates on Pasture 2S of the Santa Rita Experimental Range from 1922 to 2003. Precipitation is represented as the standardized difference (seasonal average minus the long-term seasonal average divided by the standard deviation) for four rain gauges (Box, Eriopoda, Road, and Rodent) between 1100- and 1200-m elevation. Summer (Jun to Sep) precipitation is depicted in (A) and winter (Oct to May) precipitation in (B). Annual rainfall (C) comprises winter and the following summer (Oct to Sept). Cattle stocking rates (D) are animal unit years (AUY) ha^{-1} , where $\text{AUY} = \text{number of cattle present over a calendar year}$. Data from 1965 to

1972 are not available; however, it is reasonable to assume stocking rates were ~ 0.03 (AUY) ha^{-1} prior to initiation of rotation experiment in 1972. Aerial photo dates are represented as vertical dotted lines. Periods of above-average rainfall from 1966 to 1996 are highlighted in gray.

Fig. 4. *Prosopis velutina* Woot. (Velvet mesquite) stand structure and aboveground woody biomass/carbon mass within eight 30 x 30-m plots on the Santa Rita Experimental Range (SRER) in southeastern Arizona. Plants/patch on (A) sandy ($n = 104$ patches, $n = 5$ plots) and (B) clayey ($n = 168$ patches, $n = 3$ plots) soils. All patches $> 51\text{-m}^2$ had 3 or more trees patch^{-1} . The inset in panel (B) includes summary statistics for patch metrics; superscripts denote significant differences between groups ($\alpha = 0.05$) based on Tukey's Studentized Range test. (C) Contribution of mesquite patches (by size class) to total aboveground woody plant and carbon mass (kg ha^{-1}) in plots on sandy ($n = 5$) and clayey ($n = 3$) soils. Conversion to carbon mass was performed using the weighted average of carbon content in branches, twigs, leaves, and dead mesquite components.

Fig. 5: Aerial photograph acquired February 1936 covering a 4.4-ha region of our study site on SRER in southeastern Arizona, highlighting shrub patch structure depicted in remotely sensed imagery. Panel A includes numerous *P. velutina* shrubs of various sizes; however, the algorithm in the automated supervised classification depicted multiple shrubs as a single large ($2,074\text{-m}^2$) entity (Panel B, highlighted in cross-hatching). The inability to reliably distinguish canopies of individual plants precluded us from using

time-series aerial photos to quantify changes in *P. velutina* size class distributions and biomass.

Fig. 6. Changes in mean (\pm SE) (A) percent cover and (B) patch density for velvet mesquite patches on sandy ($n = 3$) and clayey ($n = 4$) soils at $\sim 1,100$ -m elevation on the SRER in southeastern Arizona. One clayey landscape was a statistical outlier (see text for details) and is displayed separately in both panels (open triangle). Test statistics do not include the outlier. The dotted line in Panel (A) denotes the proposed maximum mesquite canopy cover proposed by Glendening (1952). X-axis alignment for sandy soils in 1966 and 1996 data points were offset slightly in panel A to display standard errors more clearly.

Fig. 7. Fate of individual mesquite canopy patches tracked on sandy (coarse sandy loam; $n = 28$ patches) and clayey (sandy clay loam; $n = 35$) soils from (A) 1936 to 1966 and (B) 1966 to 1996. Patches were hand-digitized on aerial photography and classified as exhibiting (i) no change in size, (ii) decrease in size via fragmentation or canopy die-back, (iii) increase in size via coalescence or canopy expansion, or (iv) disappearance.

Fig. 8. Proportion of 50-m^2 patches not occupied by woody patches in 1936 that were later colonized in either 1966 (A) or 1996 (B) on sandy ($n = 39$) and clayey ($n = 56$) soils. Occupied patches were scored by whether developing woody patch cover resulted from the appearance of new individuals (“recruits”) or expansion of existing canopies (“neighbor”) in the vicinity of the 50-m^2 target area. Panel B represents cumulative occupation; the proportions of patches occupied in 1966 that remained occupied are denoted as “previous.”

Fig. 9: Conceptual diagram depicting changes in woody plant cover (lines) and patch size structure (inset histograms) in two distinct phases: (1) an encroachment phase (denoted by \nearrow) with directional increases in woody plant cover and (2) a stabilization phase (denoted by $\sim\sim\sim$) characterized by patch dynamics and fluctuations in stand structure around a dynamic equilibrium. Woody plant cover was estimated by classifying aerial photographs (1936, 1966, and 1996) on two soils: sandy (black circles) and clayey (gray circles); peak clay content and depth to peak clay content given in legend in parenthesis (see text for more details). Shrub patch size distributions were delineated using natural breaks; y-axes on inset histograms correspond to the following size classes for patches: (1) $\leq 5\text{-m}^2$, (2) $6 - 10\text{-m}^2$, (3) $11 - 25\text{-m}^2$, (4) $26 - 50\text{-m}^2$, (5) $51 - 100\text{-m}^2$, (6) $101 - 250\text{-m}^2$, and (7) $> 250\text{-m}^2$. Pre-1936 dashed lines are qualitative reconstructions based on historical accounts of Wooten (1916). Stand structure (inset histograms; sandy = black and clayey = gray) was significantly different on the two soils in 1936 ($KS_a = 2.937, p < 0.0001$) and 1966 ($KS_a = 2.465, p < 0.0001$). In the stabilization phase (1966 to 1996), woody stand structure on both soils was similar and exhibited statistically significant shifts in size distributions between years (sandy $KS_a = 2.686, p < 0.0001$; clayey $KS_a = 1.804, p = 0.0030$). Dashed lines post-1996 represent hypothesized future dynamics. Hypothesized rates and trajectories are also presented for early-Pleistocene (high clay content) upland landscapes (dotted lines) on which mesquite cover has remained low (McAuliffe 1995, McClaran 2003). Two scenarios are indicated: (A) no future increases in mesquite cover due to an edaphic barrier to shrub establishment and (B) increasing shrub cover over time lagging behind that observed for soils with lower clay content.

Figures

Fig. 1.

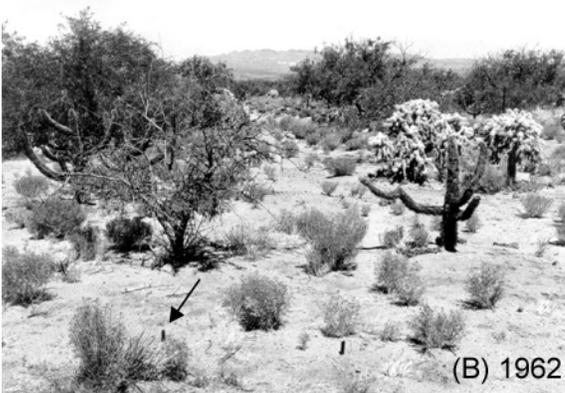
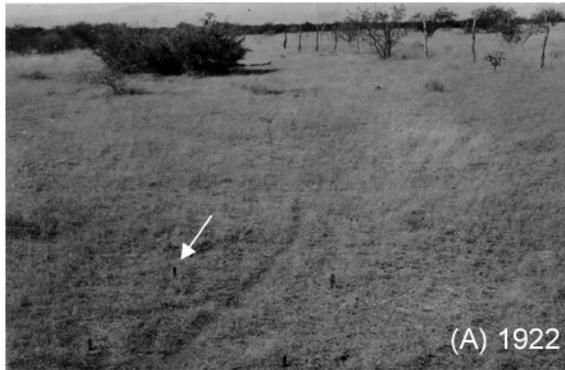


Fig. 2.

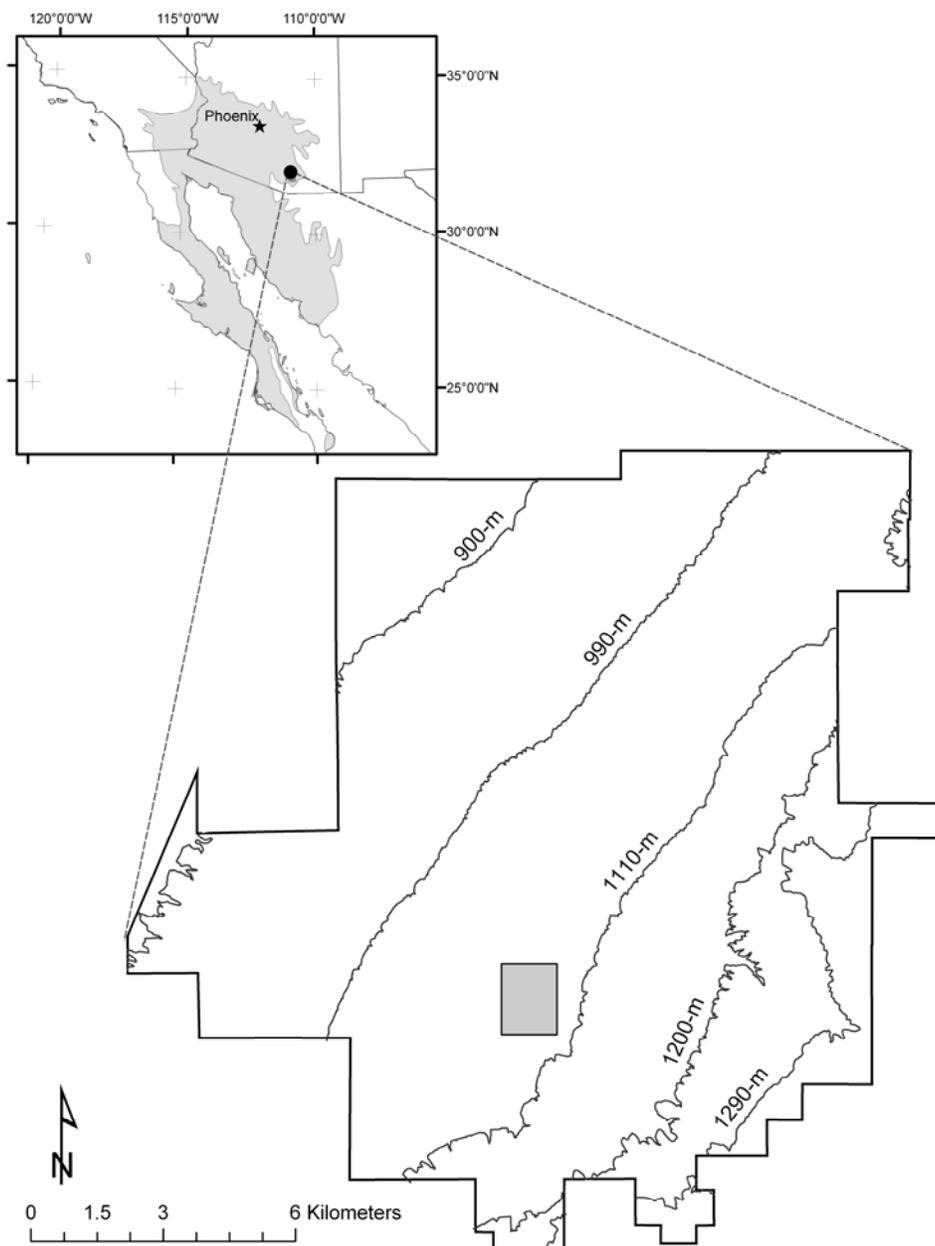


Fig. 3.

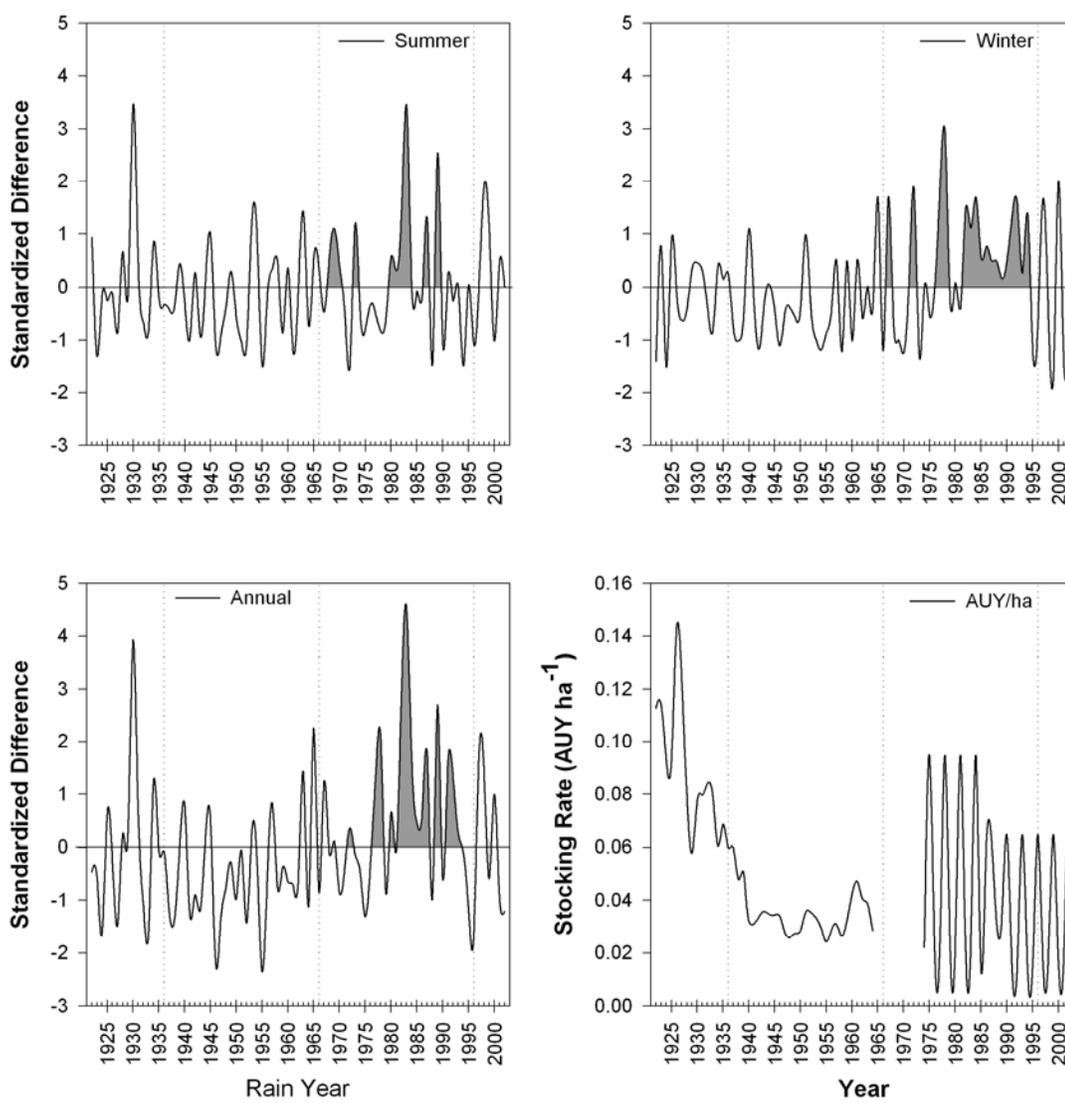


Fig. 4.

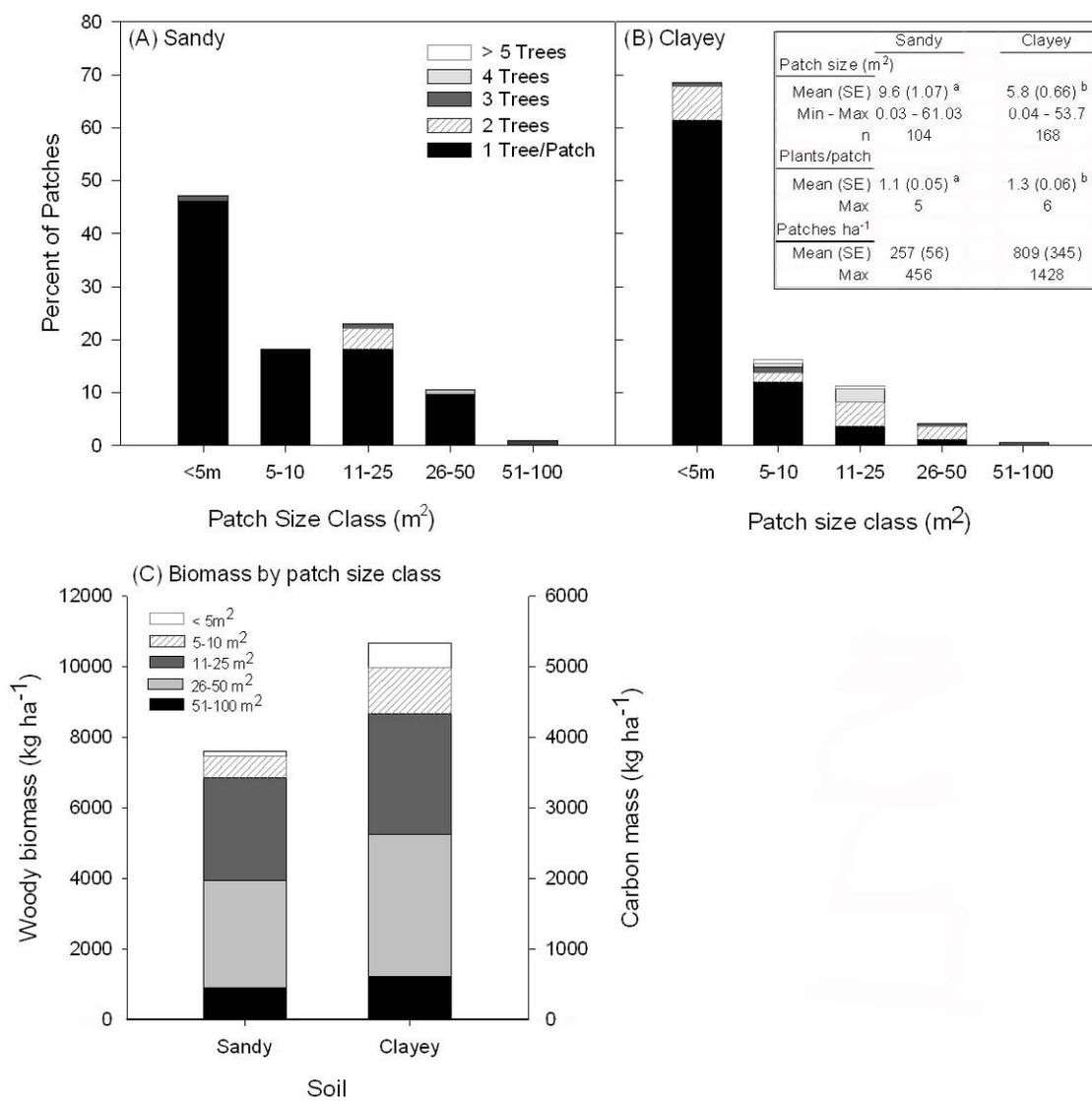


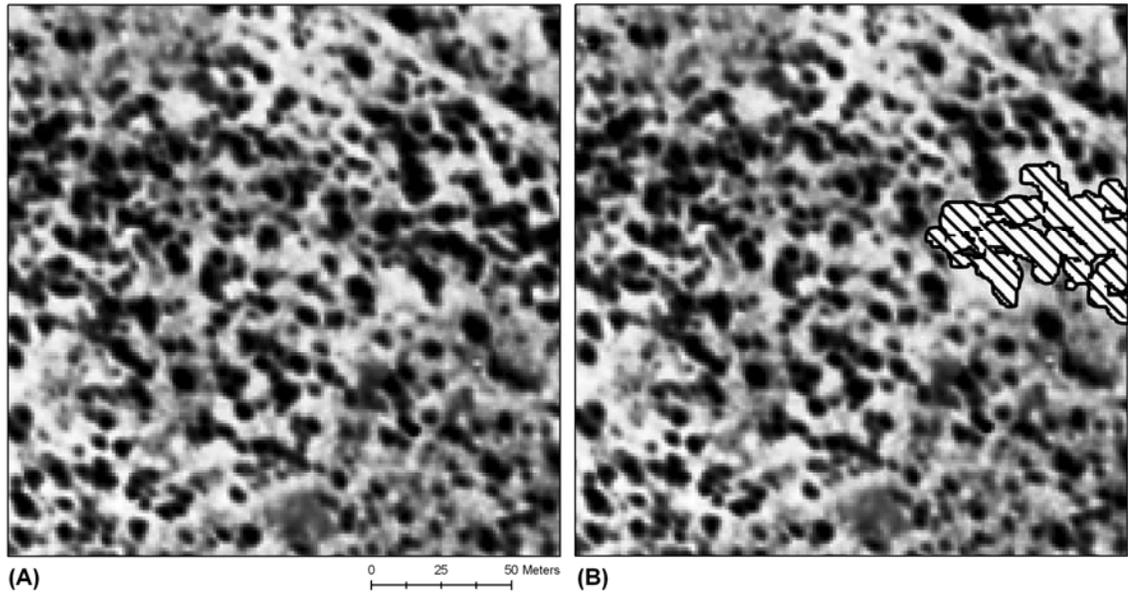
Fig. 5.

Fig. 6.

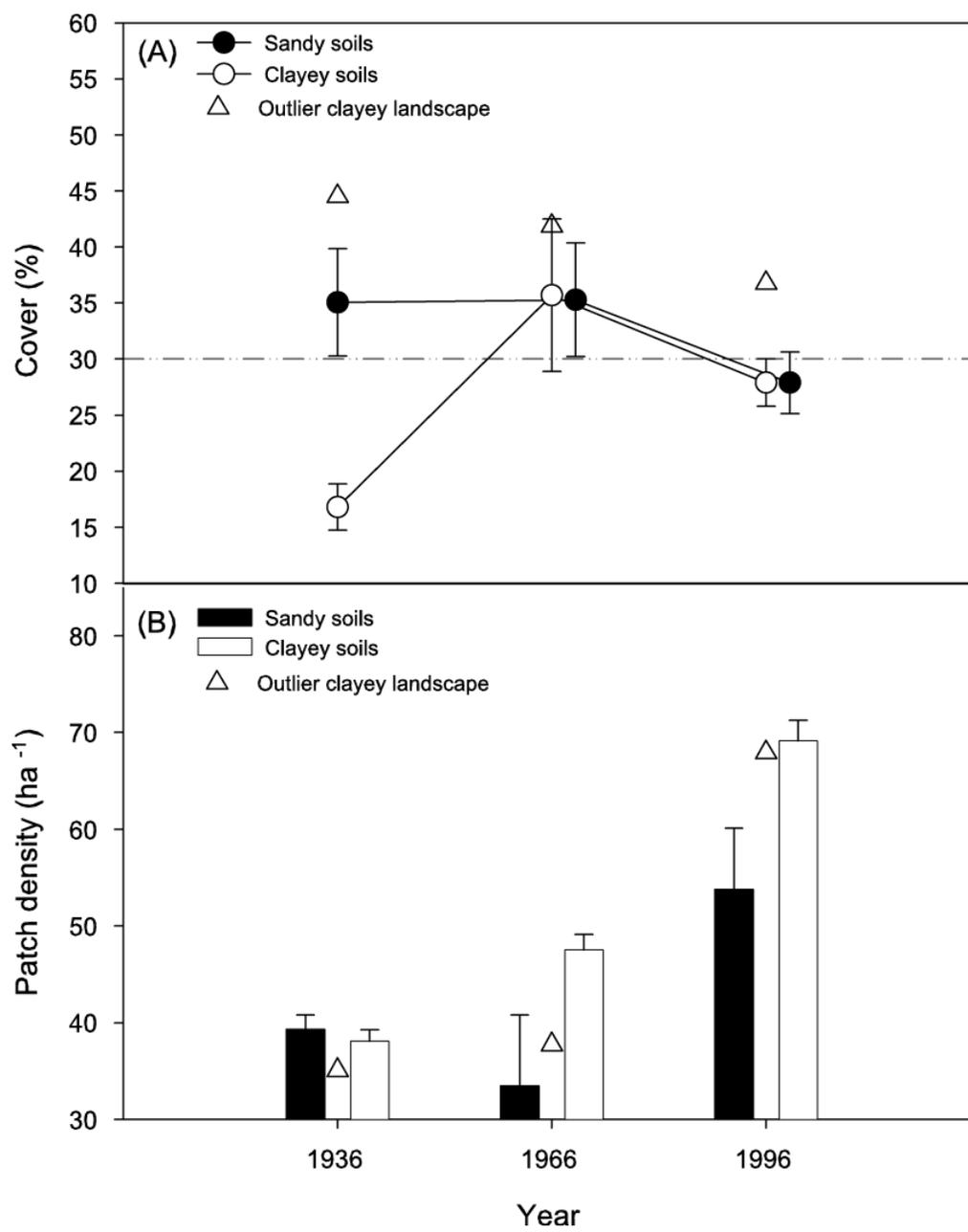


Fig. 7.

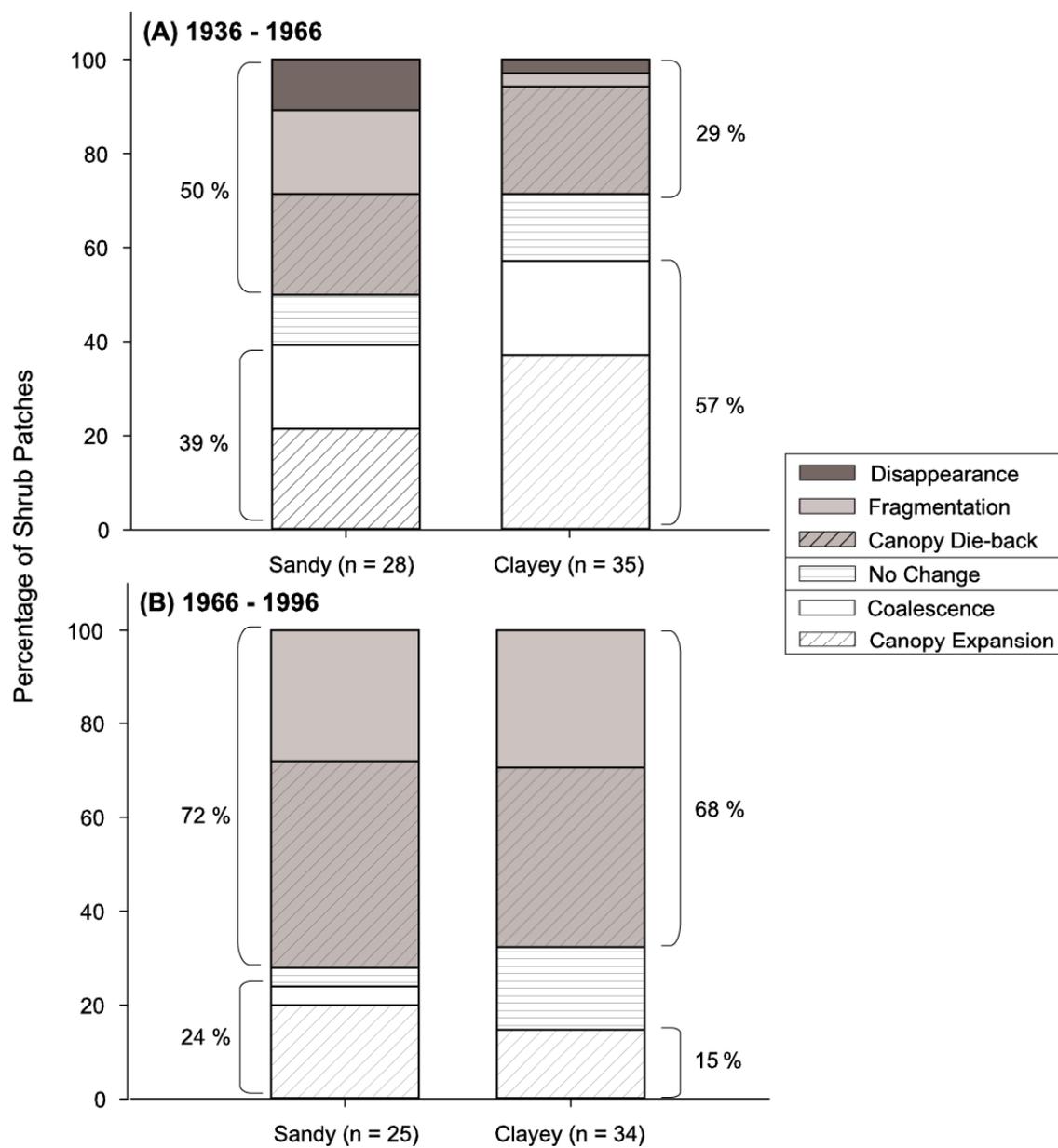


Fig. 8.

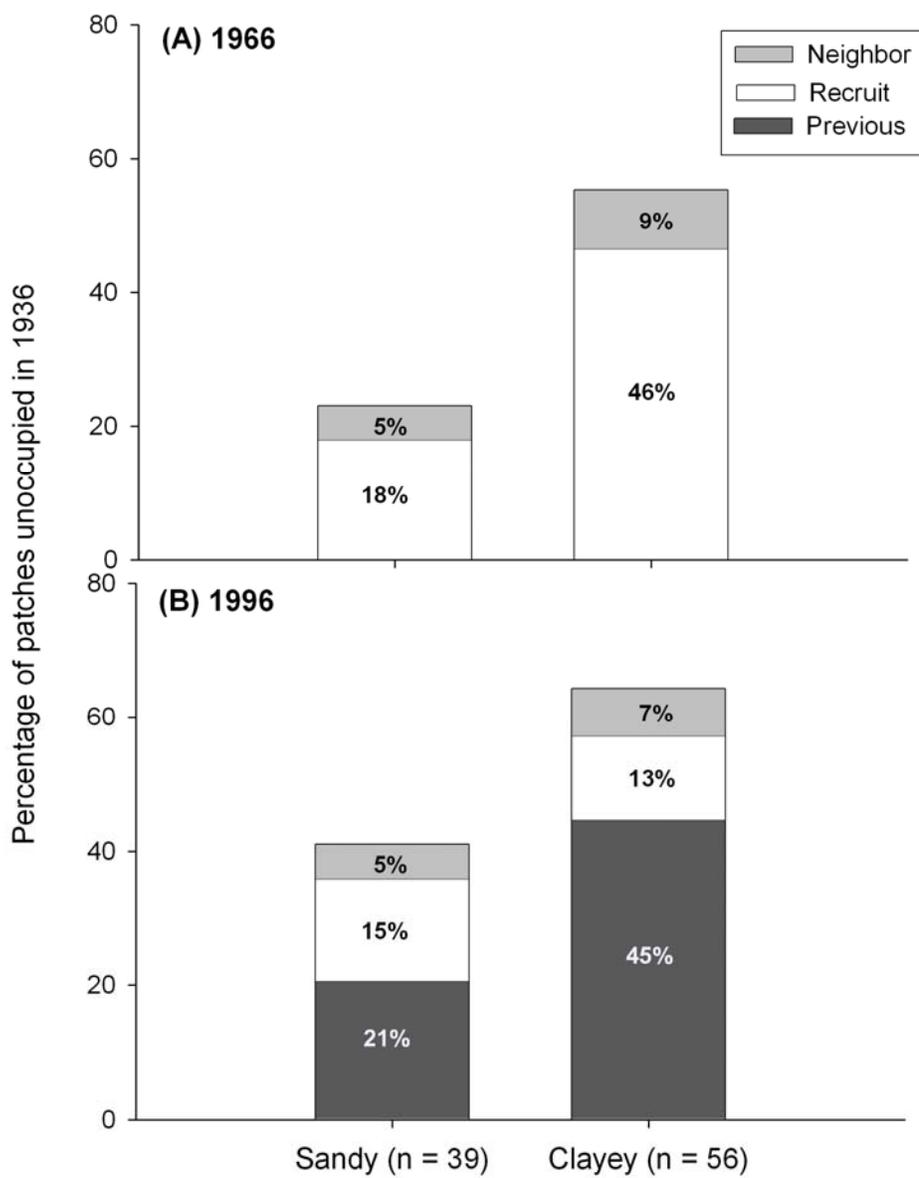
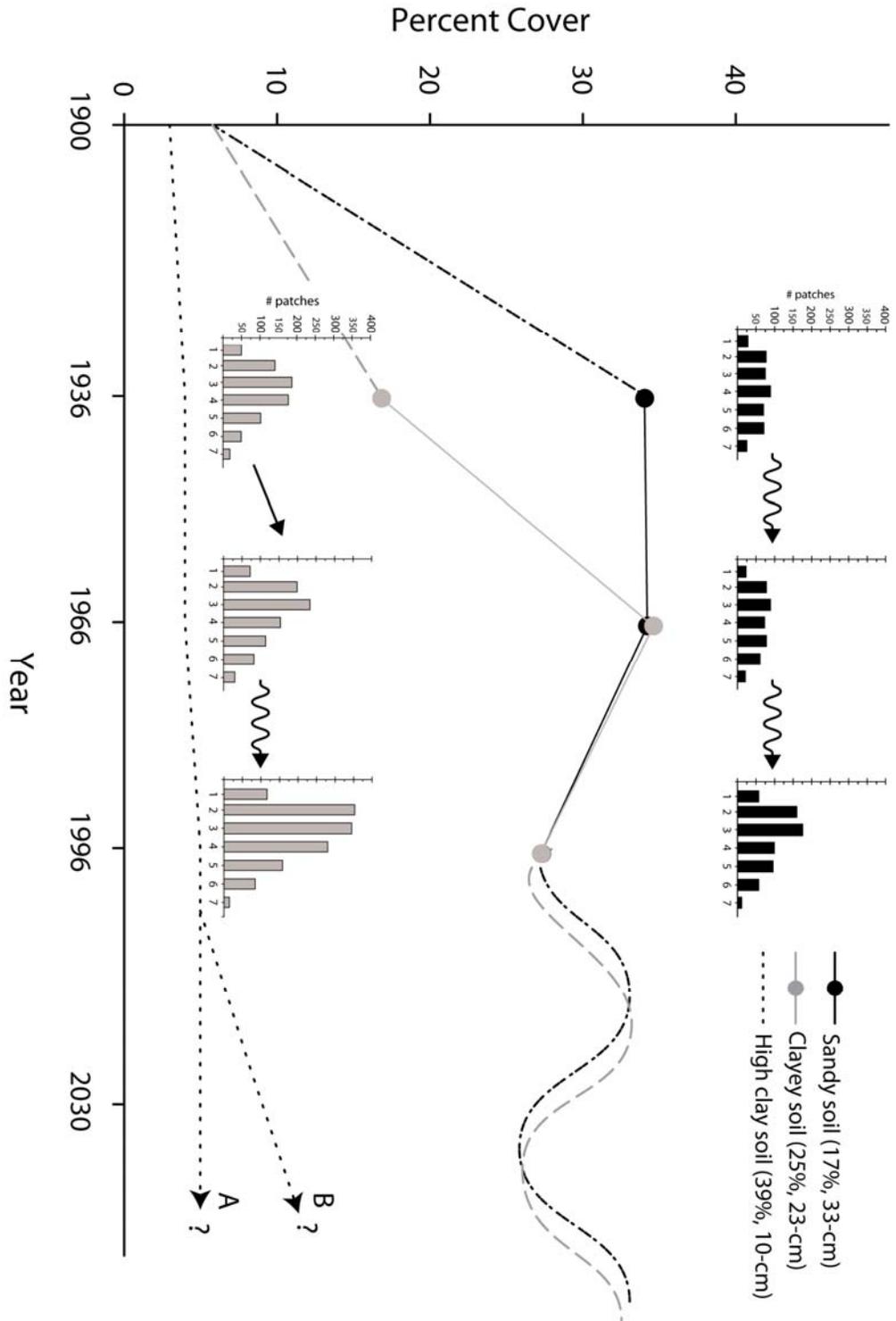


Fig. 9.



APPENDIX B

**FIELD VALIDATION OF 1930s AERIAL PHOTOGRAPHY: WHAT ARE WE
MISSING?**

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Abstract:

Aerial photography from the 1930s serves as the earliest synoptic depiction of vegetation cover. We capitalized on a well-documented land use history to generate a spatially-explicit database of stand structure for the dominant shrub, velvet mesquite (*Prosopis velutina*), within two 1.8-ha field plots established in 1932 to address two questions: (1) What are the detection limits of panchromatic 1936 aerial photography?, and (2) How do these influence *P. velutina* biomass estimates? Shrub polygons were manually digitized on 1936 imagery and linked to co-registered 1932 field measurements of *P. velutina* canopy area. Aboveground 1932 *P. velutina* biomass was estimated using a site-specific allometric relationship for field-measured canopy area. Shrub canopy detection limits on the 1936 imagery were comparable to those reported for contemporary imagery. Based on a conservative shrub size detection threshold of 3.8-m², 5.8% of *P. velutina* biomass was missed on the 1936 image. When spatial co-registration and observer bias were accounted for, 17.5% of biomass was missed. Spatial resolution (0.6- vs. 1.0-m) did not influence detection limits, but the overall accuracy of shrub cover estimates was greater on 1.0-m images. These analyses illustrate the importance of standardizing aerial photo interpretation protocols and accounting for uncertainties associated with shrub biomass estimates derived from aerial photography.

Introduction:

Changes in land cover and land use play a pivotal role in driving global change (Vitousek 1994, Pielke et al. 2002). Historical perspectives enable researchers to elucidate trends and patterns of change and to disentangle interactions among factors influencing change trajectories (Foster et al. 2003). Aerial photography is useful for making quantitative multi-temporal assessments of land cover change. The synoptic nature and length of record provide the capability to map and monitor resources over large areas at decadal time scales. The debut of widely available commercial aerial photography in the United States followed World War I (Lillesand and Kiefer 2000) is the only source of remotely sensed imagery for capturing land surface characteristics across broad scales prior to the launch of satellite sensors in the 1970s.

Land use change analyses involving remotely sensed imagery require prudent evaluation of accuracy and performance (Rindfuss et al. 2004). A valuable component of the historic record, early aerial photography provides an important source of base-line assessments for studies of land cover change and an effective way to monitor long-lived plant species in a manner not generally possible in plot or experimental studies (Archer 1996, Archer and Bowman 2002, Fensham and Fairfax 2002). The earliest aerial photography available in the southwestern United States was acquired in the mid-1930s as part of agricultural surveys conducted by the Soil Conservation Service (Bahre 1991). Because early aerial photos provide a baseline to gauge the rate and extent of land cover and land use change, insights regarding detection limitations are relevant for land

managers as well as members of the remote sensing, landscape ecology, forestry, and the ecosystem/global change modeling community. However, there are no published records documenting the detection limits and accuracy of vegetation cover estimates derived from early aerial photography due to the paucity of spatially-explicit field data coincident with photo acquisition.

One of the most striking land cover changes in grasslands and savannas (hereafter “rangelands”) worldwide over the past 150 years has been the proliferation of trees and shrubs (hereafter “woody plants”) at the expense of perennial grasses (Archer 1995, Van Auken 2000). Rangelands occupy ca. 40% of the global land surface (Bailey 1996), contribute 30-35% of the terrestrial net primary productivity (Field et al. 1998), and are inhabited by more than two billion people (Safriel and Adeel 2005). Thus, this land cover change in rangelands has ramifications for terrestrial carbon, nitrogen, and hydrologic cycles, land surface-atmosphere interactions, and human health. Although regarded as having had a significant impact on the North American terrestrial carbon sink (Pacala et al. 2001, Houghton 2003b), the lack of detailed or spatially-explicit historical records on this shift in land cover has hindered quantitative assessments.

An improvement in our ability to accurately estimate vegetation biomass across large areas is required to reduce uncertainty in terrestrial carbon pool estimates (Schimel et al. 2006). Analysis of time-series aerial photography or a combination of aerial photography and satellite imagery is one tool for addressing shortfalls in the historic land cover record (Asner et al. 2003). However, the utility of aerial photography for quantifying trends and patterns of woody plant cover in rangelands depends upon a

variety of factors, including photo scale, atmospheric haze, spatial resolution or ground-resolved distance, and film development and digital image processing protocols (Fensham and Fairfax 2002, Fensham et al. 2002). These factors can be assessed in modern photography (e.g., Fensham and Fairfax 2007, Robinson et al. 2008). In contrast, historical photography, the baseline on which rates, patterns and trajectories of change are based, is not typically amenable for validation. Thus, we are forced to assume that detection limits in early images are comparable to those in more recent images. How robust is this assumption?

Photo grain size or ground-resolved distance imposes constraints on the ability to distinguish landscape elements with remotely sensed imagery. Understanding these limitations is key to devising appropriate analytical methods to achieve study objectives (Woodcock and Strahler 1987). Strahler et al. (1986) recognized the importance of spatial scale and the interactions between scale, discrete versus continuous depictions of landscape parameters, and spatial autocorrelation structure within an image. They proposed a framework for theorizing relationships distinguished by whether study objectives pertain to targets smaller than the grain size (e.g., mapping shrub canopy cover with moderate resolution satellite imagery) or to targets larger than the grain size, such that an object comprises multiple pixels (e.g., mapping shrub canopies with fine resolution aerial photography). In our analysis of 1936 panchromatic digital imagery (defined as a H-resolution model), we specify one target, canopies of the dominant woody species (*Prosopis velutina* Woot.), to: (1) determine detection limitations of 1936 photography and translate these limits to *P. velutina* biomass missed, and (2) validate

aerial photo-based depictions of *P. velutina* canopies and landscape-scale estimates of shrub cover.

These objectives were addressed in Sonoran Desert grasslands of the southwestern USA where shrub encroachment has been well-documented (Brown 1950, McClaran 2003, Browning et al. 2008). For example, in 1932, two permanent plots (each 40-m x 440-m) were established on the Santa Rita Experimental Range (SRER) in southeastern Arizona and all woody plants (i.e., shrubs) and cacti within the plots were mapped and their canopies were measured (Glendening 1952). This provided a unique opportunity to compare field maps of shrub canopy cover in 1932 to cover maps derived from 1936 digital aerial photography. Specifically, we (1) validated estimates of shrub canopy cover at two scales of observation: *i*) individual *P. velutina* canopies and *ii*) total cover of all shrubs; (2) quantified the size of *P. velutina* plants below the detection limits on 1936 panchromatic imagery; (3) classified omission errors (*P. velutina* plants mapped in 1932 but which were not recognized on 1936 photography) attributable to *i*) detection limits, *ii*) spatial co-registration, and *iii*) species identification errors; and (4) estimated the *P. velutina* biomass missed with historic photography. In addition, we (5) quantified the effect of image spatial resolution on detection limits and cover estimates by evaluating geometrically corrected digital imagery at two cell resolution sizes common to studies of land cover change.

Methods:

Study site

The study was conducted on the 21,514-ha Santa Rita Experimental Range (SRER) 45-km south of Tucson, Arizona (31° 49' 58" N, 110° 52' 24" W) along the western edge of the semi-desert grassland region of the Sonoran Desert as defined by (Brown 1994). We focused on two 1.8-ha (40-m x 440-m) study plots at 1,070 m elevation. Established in 1932 by Dr. William McGinnies in a mesquite savanna, the vegetation in these plots was representative of the semi-desert grasslands within the southwestern U.S. The McGinnies plots were situated on soils of late Pleistocene age with a sandy clay loam subsurface texture (Batchily et al. 2003). *P. velutina* was the dominant shrub. Other shrub species in the area included *Celtis pallida* Torr. and *Acacia greggii* Gray, and the sub-shrub *Isocoma tenuisecta* Greene (Table 1). See McClaran et al. (2003) for detailed descriptions of geomorphology, vegetation, and climate.

Aerial photo validation was based on an exhaustive 1932 census of woody plant canopies within the two 1.8-ha plots situated ca. 60-m apart from each other (hereafter referred to as 'North' and 'South'). Corners of subplots (10-m x 10-m) were marked with re-bar and canopies of all shrub and cacti species were mapped and measured using a telescopic alidade and plane table (Glendening 1952). Sub-shrubs such as *I. tenuisecta* were not mapped. We geo-coded subplot corners to a Universal Transverse Mercator (UTM) projection in 2006 with a Global Positioning System (Leica GS20) using a 0.5-m horizontal positional accuracy threshold.

1932 Field measurements

Plants in the 40-m x 440-m plots were incorporated into a geographic information system (GIS) by scanning and spatially registering 1932 scaled, hand-drawn survey maps in ArcMap (v.9.0 Environmental Science Research Institute Inc. 2004). Plant locations on 1932 field maps were digitized as points and field canopy measurements (diameter in North-South direction) were used to compute canopy area as that of a circle centered on the point location. Because of their small size and low densities, cacti were not needed to validate shrub cover estimates; therefore, cacti locations were not digitized. Plant point locations (at the bole of the primary stem) were then translated to circular polygon depictions of shrub canopies by buffering points using canopy radius. Polygons representing woody plant canopies were then projected to UTM coordinate space (RMS Error = 0.270-m) in ArcMap for comparison with canopies digitized on the 1936 photography.

To assess validity of our assumption that *P. velutina* canopies were circular, we made eight measurements of canopy radii (cardinal and inter-cardinal directions) on 26 randomly selected *P. velutina* plants in 2006. Perimeter values for polygons generated from these field measurements and for circles of the same area were highly correlated ($r = 0.998$).

Prosopis velutina biomass

Aboveground biomass (leaves +stems) of mesquite plants measured in plots in 1932 was estimated using an existing site-specific canopy area allometric algorithm (see Browning et al. 2008). The proportion of *P. velutina* biomass potentially missed on photos across a range of detection thresholds was derived using the cumulative distribution of *P. velutina* plant mass across the range of canopy sizes.

1936 Aerial photography

Film negatives of panchromatic February 1936 aerial photographs (1:31,640) were acquired from the U. S. National Archives and scanned at 1200 dpi. The image with center coverage of the McGinnies plots was subset, geometrically-corrected, and registered to the UTM projection using 40 ground control points associated with an ortho-rectified base image from the U.S. Geological Survey (Root Mean Square Error = 0.002-m). Vignetting effects (distortion along photo frame edges) were minimized by using a single image with study plots located near the center. Geo-coded 1936 images were generated at two cell resolutions corresponding to those commonly used to monitor vegetation change (Laliberte et al. 2004, Robinson et al. 2008): 0.6-m and 1.0-m. These were then used to evaluate the effect of spatial resolution on detection limits and estimates of woody plant cover.

We established a protocol to standardize what constitutes a shrub canopy (to be digitized) and the level of detail used to delineate shrub polygons. Using this protocol, we then isolated the effects of spatial resolution on detection limits of the 1936 aerial

photography. To minimize observer bias one author (AB) digitized all shrub polygons within the study plots on the 0.6- and 1.0-m resolution images using ArcMap. To maintain consistent detail in creating polygons, the digitizing process was performed in stream mode, which places vertices every 2-m along the patch perimeter. Pre-defined magnification levels were implemented to identify shrub canopies on the 1936 images, balancing magnification level and the ability to confidently discern canopies and their outlines. Discernable shrubs were initially identified by heads up digitizing canopies at magnifications 1:1,250 or 1:800. Once canopies were identified, their size and shape were refined on the basis of color and texture differences with surrounding pixels. Area and perimeter for manually digitized canopies were derived in ArcMap using Hawth Tools, a set of geoprocessing tools integrated with ESRI software (Beyer, H.L. 2004).

Image validation and error categorization

The shrub cover map digitized from the 1936 image was overlaid on the 1932 field map of shrub canopies to determine the extent to which the aerial photo estimates approximated field-based estimates (Fig. 1). In addition to identifying plants not recognized on 1936 image, we assessed two common types of error in photo interpretation: data co-registration and observer error. Co-registration errors corresponded to the inability to confidently link digitized canopies on the photo to non-overlapping plant canopies on field maps. We defined observer error in the photo interpretation process as selective discrimination in what was defined as a plant canopy on the 1936 image. Cases of observer error occurred amidst medium tone or color that

lacked texture or discrete shape, such as might coincide with dense herbaceous cover. *P. velutina* plants mapped in 1932 not corresponding to a 1936 digitized canopy were categorized as missed because: (1) they were below detection limits (i.e., the observer had no indication a *P. velutina* canopy was present), (2) of spatial co-registration error, or (3) the color, shape, and texture of the canopy was not sufficiently distinct to warrant classifying as ‘shrub.’ In the comparison of field- vs. image-generated maps, small *P. velutina* plants beneath canopies of larger plants ($n = 14$ of 604) were excluded from the analysis of detection limitations, but were included in estimates of *P. velutina* biomass missed with 1936 photography.

Validation of aerial photo woody cover estimates

To what extent can historical aerial photography be used to ascertain the canopy area of individual shrubs, and thus characterize the size-class distribution of plants on a site? How accurately does historic aerial photography depict woody plant cover at larger spatial extents? To address these questions, we verified photo estimates at two spatial scales: individual *P. velutina* canopies and shrub cover within 1.8-ha plots. We compared measurements of plant canopy area derived from 1936 photography at 0.6- and 1.0-m resolutions to field measurements of plant canopy area in 1932 using linear regression. We limited canopy size validation to single *P. velutina* plants whose canopies on field maps were separated from the canopies of their neighbors by at least 1-m.

At the landscape-scale (i.e., both study plots), spatial heterogeneity in vegetation cover, species composition, and plant density influence total cover estimates on aerial

photos. To assess landscape-scale estimates of total woody cover, we compared estimates from 1936 photos at 0.6- and 1.0-m spatial resolutions to that on 1932 field maps. In this landscape-scale assessment, boundaries of overlapping shrub canopies on field maps were dissolved to represent woody plant cover from an aerial, top-down perspective and portions of shrub canopy polygons on photos and field maps beyond plot boundaries were excluded, such that % woody cover = total shrub canopy area within plot (m²)/plot size (m²).

Species contributions to total woody plant cover were generated following the manual assignment of digitized 1936 shrub canopies on 0.6- and 1.0-m imagery to species-specific field data. To standardize the species identification process, we applied a 1-m buffer to dissolved 1932 field polygons. When 1936 photo-canopies overlapped 1932 field canopies within one meter and canopy size and position corresponded, the digitized canopy was assigned the woody species value. If a 1936 digitized canopy did not overlap with the 1-m buffered 1932 canopy locations and/or digitized canopies did not correspond in shape or size to a mapped 1932 woody plant canopy (including all mapped species), it was labeled “Other.”

Results:

Detection limits

P. velutina plants not discernable on the 1.0-m image were also not discernable on the 0.6-m image. Thus, spatial resolution did not significantly influence detection limits of individual plant canopies. Canopy area of undetected plants ranged from 0.01 to 9.6-

m². Mean (± 1 SE) canopy size of undetected *P. velutina* plants on the North plot (1.7 ± 0.3 -m²) was significantly greater than that of plants on the South plot (0.9 ± 0.2 -m²; $t = 2.37$, $df = 46$, $p = 0.021$) and variances associated with means were unequal (folded $F = 2.3$, $df = 47$, $p = 0.002$). Therefore, results were not pooled (Fig. 2A). Sizes of 1932 *P. velutina* canopies not linked to 1936 digitized canopies due to data co-registration and observer error are summarized in Fig. 2B. When omissions related to co-registration and observer error were accounted for, the maximum canopy size missed was 19.6-m².

To illustrate the influence of detection limitations on estimates of *P. velutina* aboveground biomass, we used a 3.8-m² canopy area detection threshold. This represents the 90th percentile for canopies not detected on 1936 images (inset, Fig. 2A) and limits the undue influence of the largest plants. Using this threshold, canopies ≤ 3.8 -m² comprised 5.8% of *P. velutina* biomass ($n = 436$, Fig. 3). Potential errors associated with other canopy area detection thresholds, as might occur with images of a different film type, quality, or photo scale, are also shown in Fig. 3.

Validation of aerial photo woody cover estimates

P. velutina canopies digitized from the 1936 aerial photo rendered statistically significant representations of field-measured canopy sizes at both 0.6-m ($F = 35.57$, $df = 46$, $p < 0.0001$) and the 1.0-m ($F = 35.51$, $df = 44$, $p < 0.0001$) resolutions. The canopy area of individual *P. velutina* plants was consistently underestimated at the 0.6-m resolution (Fig. 4A), whereas canopies on the 1.0-m image were both under- and over-estimated and more closely approximated a 1:1 relationship with 1932 field

measurements (Fig. 4B). Given that the 1932 field canopy measurement values in Fig. 4 are fixed (x-axis); differences in photo-derived estimates of *P. velutina* canopy area reflect the influence of spatial resolution on aerial photo interpretations.

Total shrub cover differed on the North and South plots, as did the contribution of less common species; however, *P. velutina* clearly dominated woody plant cover (Fig. 5, Table 1). At the landscape scale, total shrub cover was underestimated on the 0.6-m image by 37% (North plot) and 38% (South plot). At the 1.0-m resolution, shrub cover was overestimated by 5% on the North plot and underestimated by 13% on the South plot, where mean *P. velutina* canopy size was statistically smaller than that on the North plot (Fig. 2A). Contributions of *Celtis pallida* (North plot) and *Acacia gregii* (South plot) were accurately depicted at both spatial resolutions. Relative contributions of unidentified species to absolute shrub cover, consistent for 0.6- and 1.0-m images, ranged from 26% to 33% of total cover (Fig. 5). What might constitute this surprisingly large portion of shrub cover?

Species composition of ~ 70 polygons classified as ‘Other’ on the 1936 photography (Table 2) was possibly: (1) cacti (*Opuntia fulgida*, *O. spinosior*, *O. engelmannii*, *Echinocactus wislizeni*), (2) large patches of dense herbaceous ground cover, or (3) the sub-shrub, *Isocoma tenuisecta*. The composition of the unknown patches was likely not cacti because: (1) a visual inspection of cacti locations on geo-coded field maps indicated cacti locations did not spatially coincide with ‘Other’ image patches and (2) cactus density in 1932 was extremely low - 30 plants ha⁻¹ (Glendening 1952). Composition of ‘Other’ was likely not herbaceous vegetation as average ground

cover was only 0.84% on the mapped study plots (Glendening 1952). However, the composition of ‘Other’ may have been *I. tenuisecta*. Canopies of this sub-shrub can approach detection limits [Fig. 6, SRER Archives (McClaran et al. 2002)] and multi-plant patches of this sub-shrub might be readily detected.

Discussion:

Aerial photography from the 1930s provides the earliest synoptic, large-scale records of land cover. The use of such photos to establish baseline conditions from which to gauge subsequent change requires knowledge of the extent to which the optical and film technologies in use at that time can accurately depict land surface features of interest. In our case, we were interested in using early imagery as a baseline from which to reconstruct the rate and magnitude of changes in shrub cover and biomass in areas that were historically grasslands. By incorporating 1932 field maps of shrub canopies at the SRER generated by Dr. William McGinnies into a spatially-explicit database, we were able to take advantage of a unique opportunity to critically evaluate the accuracy and limits of 1936 aerial photos for this purpose.

Detection limits of 1930s aerial photography

The minimum mapping unit in remote sensing studies is typically defined by the pixel (i.e., grain) size of imagery (e.g., Goslee et al. 2003). Our analyses suggest this assumption is too simplistic for 1936 panchromatic aerial photography where detection limits for our targets of interest (shrub canopies) were nearly four times the grain size. We found a substantial range of sizes of ‘undetected’ shrub canopies, but using a 90th

percentile cutoff generated a minimum canopy area detection size of 3.8-m². This result compares favorably with detection limits ranging of 2.9- to 3.3-m² canopy area reported for woody plants in 1994 natural color digital imagery (1.4-m resolution) in Western Australia (Robinson et al. 2008). In our manual classification of 1936 imagery, we ‘missed’ three large *P. velutina* plants whose canopies were indistinguishable from the background herbaceous matrix. Close inspection of field data and the spatial context of these individuals did not reveal an obvious reason for their misrepresentation. However, these plants constituted only 0.07% of total shrub canopy area and 0.64% of total *P. velutina* cover. These outliers highlight the importance of evaluating the distribution of canopy sizes not represented rather than simply choosing the maximum value to define the minimum mapping unit. Thus, from a minimum detection limit standpoint, the 1936 imagery proved comparable to what can be obtained in more modern images.

Field validation of woody plant cover

Our validation of shrub cover estimates from 1936 panchromatic aerial photography conducted at two spatial scales revealed that biases at the level of individual canopies are translated to depictions of cover at the landscape scale; that total plant cover can be accurately delineated; and that caution must be exercised when using it for species-specific cover or biomass assessments. Effects of shadow on photo-derived estimates of canopy area and shrub cover occur at both individual canopy and landscape scales. Metadata needed to permit correction for shadow and atmospheric conditions were unavailable, as is commonly the case with archive aerial photography (Linda

Cullemer, U.S. National Archives, *pers.comm.*). However, the correspondence between field-measured and 1.0-m photo image canopy areas suggests shadow on the 1936 image may not have been significant. Flat terrain (<3% slope) and the February acquisition date (when the deciduous shrubs would have been largely leafless in this semi-arid system) likely helped downplay the effects of shadow. Furthermore, shadow effects typically result in overestimation of crown area (Fensham et al. 2002), not underestimation as in our case. It appears that color-texture distinctions between shrub canopies and background plants and soils were blurred at the 0.6-m resolution in a manner that caused shrub canopy area to be underestimated.

Canopy-scale comparisons

Relative to the 0.6-m image, the 1.0-m spatial resolution yielded better estimates of area at the level of individual canopies. Shrub canopies on the 0.6-m image were consistently underestimated. This result is counterintuitive to the expectation of enhanced image detail with finer spatial resolution; however, it corroborates results from Fensham and Fairfax (2007) who also observed that shrub canopies appear larger as photo scale decreases (i.e., coarsens). For the 1:31,640 imagery used in this study, the 1.0-m resolution appeared to provide optimal results.

The correspondence between field- and photo-measured areas of individual plant canopies ($R^2 = 0.45$) was at the lower range of that reported for calibrations of woody plant cover on 2004 color aerial photos of *Acacia* and *Eucalyptus* woodlands in Australia ($R^2 = 0.50$ to 0.91 ; Fensham and Fairfax 2007) and for 2004 digital multispectral images

of *Prosopis* spp. in Western Australia ($R^2 = 0.98$; Robinson et al. 2008). However, our field validation of photo-derived shrub cover was rigorously conducted at the scale of individual canopies, appropriate for quantifying woody stand composition and structure. The aforementioned validation outcomes were conducted using plot-scale cover estimates where shadow and halation (point spread function of dark canopy against bright surrounding matrix) effects are averaged across the entire study area. Thus, it is to be expected that estimates of percent cover will exhibit less variability than estimates of individual plant canopy area. In our case, aerial photo estimates of the canopy area of individual *P. velutina* plants may have been biased by the failure to account for canopies of *I. tenuisecta* in the 1932 field survey. If we were detecting large patches of this subshrub on the aerial photography; or if *I. tenuisecta* patches were adjacent to *P. velutina* plants or occurred near canopy edges (Fig. 6), then this could potentially explain some of the over-estimates of canopy area in Fig. 4B.

Discrepancies between photo- and field-maps of shrub cover can occur if photo acquisition and field measurement dates differ and are not accounted for (Fensham and Fairfax 2002). Based on estimates of canopy expansion rates at this site [$0.25 \text{ m}^2 \text{ y}^{-1}$, Browning et al., 2008], the four intervening years from field data collection and image acquisition could have resulted in an approximate 1-m^2 increase in *P. velutina* canopy area. Canopy growth between 1932 and 1936 would result in overestimates of canopy size in the photography. We could not evoke potential canopy growth over four years to explain variability in canopy size estimates, as photo-measured *P. velutina* canopy size was not consistently overestimated. Furthermore, this small adjustment would have

minimal effect on the overall spread of points in Fig. 4, particularly for the larger (canopy area > 20-m² area) plants.

Landscape-scale comparisons of cover

Effects of spatial resolution on accuracy of shrub cover estimates evident at the landscape scale are likely due to a combination of factors such as stand size structure and shrub species identification. The degree of underestimation of total *P. velutina* cover (Fig. 5) was, to some extent, a function of the abundance of plants at or below detection limits. *P. velutina* plants on the South plot were smaller than those on the North plot (Fig. 2A); therefore *P. velutina* cover missed with the photography was somewhat greater on the South plot. The close correspondence between field and photo estimates of total shrub cover at 1.0-m appears to reflect the fact that underestimates of *P. velutina* cover, due in part to detection limitations, were compensated for by the contribution of ‘Other’ vegetation patches on the photo that were not mapped in the 1932 field census.

Unidentified vegetation patches that compensated for underestimates of *P. velutina* cover represent a challenge for retrospective interpretation of historic aerial photography. Historical records and ground photography (Fig. 6) suggest the sub-shrub *Isocoma tenuisecta* was the most likely species to contribute to the ‘other’ vegetation patches. This plant exhibits strong cyclic patterns of population growth and decline (McClaran 2003, McClaran and Angell 2006). In 1934, the 5-km² area encompassing the McGinnies plots was classified as “heavily infested” with *I. tenuisecta* with over 3,707 plants ha⁻¹ (Mehrhoff 1955, Humphrey and Mehrhoff 1958). Had the cover of this

species been accounted for in the 1932 field map, 1936 photo estimates of total woody cover may thus have been underestimated to a somewhat greater extent than what is shown in Fig. 5. It seems reasonable to expect that conglomerate patches of this plant may have been evident on the 1936 image. The presence of plants such as *I. tenuisecta*, which is intermediate in growth form and longevity between herbaceous and a true (fruticose) shrub, may further complicate species-specific interpretation of cover and biomass estimates.

Ramifications for biomass estimation

Remote sensing has great potential for estimating terrestrial biomass across large areas at relatively low cost (IPCC 2003), yet challenges remain for widespread application (Lu 2006). We highlight three issues related to spatial resolution with the use of historic aerial photography for mapping woody plant biomass in arid rangelands and address each challenge for quantifying plant biomass in turn.

First, the majority of remotely sensed imagery is not capable of discerning the smallest members of the plant community, thereby missing the most dynamic portion of the population and greatly compromising the ability to represent woody plant size class distributions. Although plants below detection thresholds (canopies $< 3.8\text{-m}^2$ in our case) constituted only a small fraction of the total shrub biomass (ca. 6% in our case), the inability to detect this portion of the plant population compromises our ability to forecast ecosystem productivity and carbon sequestration potential because carbon uptake is maximal in young stands and plateaus in mature stands (Hurt et al. 2002).

Second, assumptions regarding species or functional group composition should be clearly stated and, to the extent possible, evaluated. Species identification is rarely attainable remotely; and in this regard, our findings present no new case. Our original intent was to use estimates of aboveground biomass derived from shrub canopy cover on 1932 imagery as a baseline from which to quantify rates and patterns of change using aerial photos in subsequent decades. Because *P. velutina* clearly dominated cover on the study site (Table 1) we assumed we could apply a canopy-area biomass algorithm developed for this species across the site. Although this algorithm would not necessarily be appropriate for other species on the site, 1932 field maps and more contemporary field surveys indicated their abundances were low enough that errors would be minimal. However, as it turned out, 26-33% of the classified shrub cover on the 1936 image was attributable to ‘Other’ species, probably *Isocoma tenuisecta*, not reported in field maps. Using species-specific algorithms, a 5-m² canopy (2.5-m canopy diameter) *P. velutina* plant would have 7.3-Kg dry weight aboveground biomass (allometric relationship from Browning et al. 2008), whereas an *I. tenuisecta* sub-shrub of comparable canopy area would have a mass of 6.1-Kg (allometric relationship from Huang et al. 2007). Thus, if *I. tenuisecta* comprised the ‘Other’ fraction of total shrub cover and the *P. velutina* algorithm was applied, aboveground woody biomass would be over-estimated by ca. 20%. In the absence of metadata, there is little recourse in correcting these errors on old aerial photographs. However, these data suggest modern estimates may need to be supplemented with field surveys and enhanced through retrospective mapping to

determine species composition (Andersen 2006) or remote sensing tools that could inform judgments about species or functional group composition and relative abundance.

Finally, the inability to discern individual plant canopies in satellite or airborne imagery is a function of the spatial and spectral resolution of the sensor, shadow, canopy architecture, and plant density. In cases where canopies of individual plants of the same or differing species meet or overlap, it cannot be reliably determined from a top-down perspective whether a given entity represents one large plant, multiple plants of the same species, or multiple plants of differing species. We circumvented this problem (Figs. 3 and 4) by focusing our analyses of canopies digitized on the aerial photos known to correspond to single *P. velutina* plants mapped in 1932 and limiting application of the species-specific allometric algorithm to field measurements of individual *P. velutina* canopies. For many woody plants, including *Prosopis*, biomass increases exponentially with canopy area (Northup et al. 2005). Thus, representing an entity as a single large plant, when it is in fact a group of smaller plants would have the potential to substantially overestimate biomass. This problem is not unique to the 1930s photography; and it also presents challenges for more recent aerial photography (Browning et al. 2008). Resolution of this problem may not be possible on historical photos, but contemporary estimates of biomass from remotely sensed imagery could be potentially improved by incorporating field surveys or LIDAR-based estimates of shrub height and patch structure (e.g., Vega and St-Onge 2008).

Summary

Rangelands, undergoing shifts from grass- to woody plant-domination across broad spatial extents, are a special case for efforts aimed at tracking changes in aboveground biomass estimates (Knapp et al. 2008). Advances along these lines have important consequences for reducing the considerable uncertainty in estimates of aboveground terrestrial carbon pools worldwide (Houghton et al. 1999). Repeat aerial photography is a potential tool for reconstructing change in woody plant cover and biomass in rangelands. Aerial photos from the 1930s can be used to establish baseline conditions from which to assess rates and patterns of subsequent change. Taking advantage of a historic spatially-explicit field dataset from 1932, we were able to quantify the detection limitations and accuracy of woody cover and biomass estimates from 1936 aerial photography. Spatial resolution did not influence detection limits, but the overall accuracy of shrub cover estimates was greater on 1.0-m than on 0.6-m resolution images. Overall, the information extracted from historic 1932 aerial photo images was on par with what can be extracted from aerial photos from more recent years. Our assessment of the ramifications of inherent detection limitations of 1936 aerial photography for woody plant biomass provides a starting point for delineating boundaries for broad-based assessments of woody biomass in arid rangelands with remote sensing.

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Tables:

Table 1: Number and canopy area (mean, minimum and maximum; m²) of woody plant species within two (North, South) 1.8-ha plots in 1932; data collected by Dr. William McGinnies (SRER Archives).

	North plot				South plot			
	No. of plants	Mean (SE)	Min	Max	No. of plants	Mean (SE)	Min	Max
<i>Prosopis velutina</i>	308	5.23 (0.49)	0.01	63.62	296	3.36 (0.32)	0.01	38.49
<i>Acacia gregii</i>	5	2.05 (0.76)	0.79	4.91	17	2.79 (0.76)	0.01	10.18
<i>Celtis pallida</i>	3	18.04 (9.83)	0.28	34.21	2	3.73 (3.34)	0.38	7.07
<i>Mimosa aculeaticarpa</i> var. <i>biuncifera</i>	0	--	--	--	1	--	0.13	0.13
<i>Ephedra trifurca</i>	0	--	--	--	4	0.65 (0.09)	0.38	0.79
<i>Ziziphus obtusifolia</i>	3	3.81 (1.99)	0.20	7.07	1	--	4.91	4.91

Table 2: Descriptive statistics for patches manually digitized on 1936 aerial photography at two spatial resolutions that did not correspond to the shrub species noted on 1932 field maps (see Table 1). In our species identification scheme, these patches were > 1-m from the canopy edge of mapped species and were classified as “Other.”

Patch size (m²)	Image Resolution			
	0.6-m		1.0-m	
	North	South	North	South
<i>n</i>	40	32	39	30
mean	5.9	6.6	10.6	9.1
SD	4.2	4.4	6.8	4.7
min-max	0.9-20.1	1.5-20.2	1.6-31.5	3.5-23.6

Figure Legends:

Fig. 1. Flow chart for validating shrub cover, *P. velutina* biomass, and detection limits on 1936 panchromatic aerial photography using 1932 field maps of shrub canopies in two 1.8-ha plots. Shrub species occurring in the plots are listed in Table 1.

Fig. 2. Box and whisker plots of 1932 of *Prosopis velutina* canopies missed on panchromatic (1:31,640) aerial photography acquired February 1936. Mean canopy area is illustrated with dotted horizontal lines. Inset table shows descriptive statistics for *P. velutina* plants not visible on photography. Canopies beyond the 90th percentile are represented with symbols. Panel (A) depicts the size of plants that were not visible on the imagery. Panel (B) depicts the size of known canopies from 1932 field maps missed due to two common errors in photo interpretation. Canopies that were not perceived as discrete image objects (stars ★) and those that did not overlap with digitized shrub canopies (triangles ▲). The same plants were missed at 0.6- and 1.0-m pixel resolutions.

Fig. 3. Canopy size distribution (0.5-m² intervals; bars) and cumulative *Prosopis velutina* aboveground biomass (line) based on 1932 field measurements in southeastern Arizona. Biomass was derived using an allometric equation (Browning et al. 2008). Dashed lines denote the number of plants and the proportion of *P. velutina* biomass potentially missed as a function of three canopy area detection thresholds (5-, 15-, and 30-m²).

Fig. 4. Relationship between shrub canopy area manually digitized from panchromatic 1936 aerial photography (y-axis) and 1932 field-measured *Prosopis velutina* canopy area (x-axis) at two spatial resolutions: 0.6-m (A) and 1.0-m (B). Field measurements (x-axis)

are the same in both panels; hence differences in 1936 photo-derived canopy area reflect differences resulting from differences in spatial resolution. Only canopies corresponding to a single *P. velutina* plant were used in this analysis; multiple-plant patches were excluded. Dotted lines represent one-to-one relationship.

Fig. 5. Species-specific contributions to woody plant cover at the Santa Rita Experimental Range in southeastern Arizona, as determined from 1932 field measurements (Table 1) and 1936 aerial photography manually digitized at two (0.6- and 1.0-m) resolutions for two 1.8-ha plots (North and South). Species assignments on the 1936 photograph were made by overlaying species-specific field projections of canopy area onto digitized polygons. Polygons classified as ‘shrubs’ but not corresponding to woody plants on the 1932 field maps were categorized as “Other.” Relative (%) species contributions to absolute cover are indicated within each bar. Contributions of *Ephedra trifurca* and *Ziziphus obtusifolia* to total cover (not shown) were 0.01% and 0.03%, respectively.

Fig. 6. Dr. Robert R. Humphrey with a burro weed plant (*Isocoma tenuisecta*) 21 February 1935 [photo by Gibbs, Santa Rita Experimental Range Archive (No. 328920)]. Photo was taken adjacent to South McGinnies plot. Assuming a 2-m arm span, this subshrub would have a canopy area of ca. 3.1-m² in size, approaching the detection limits of the 1936 aerial photography. Widely scattered *Prosopis velutina* trees appear in the background within a grassy matrix.

Figures:

Fig. 1

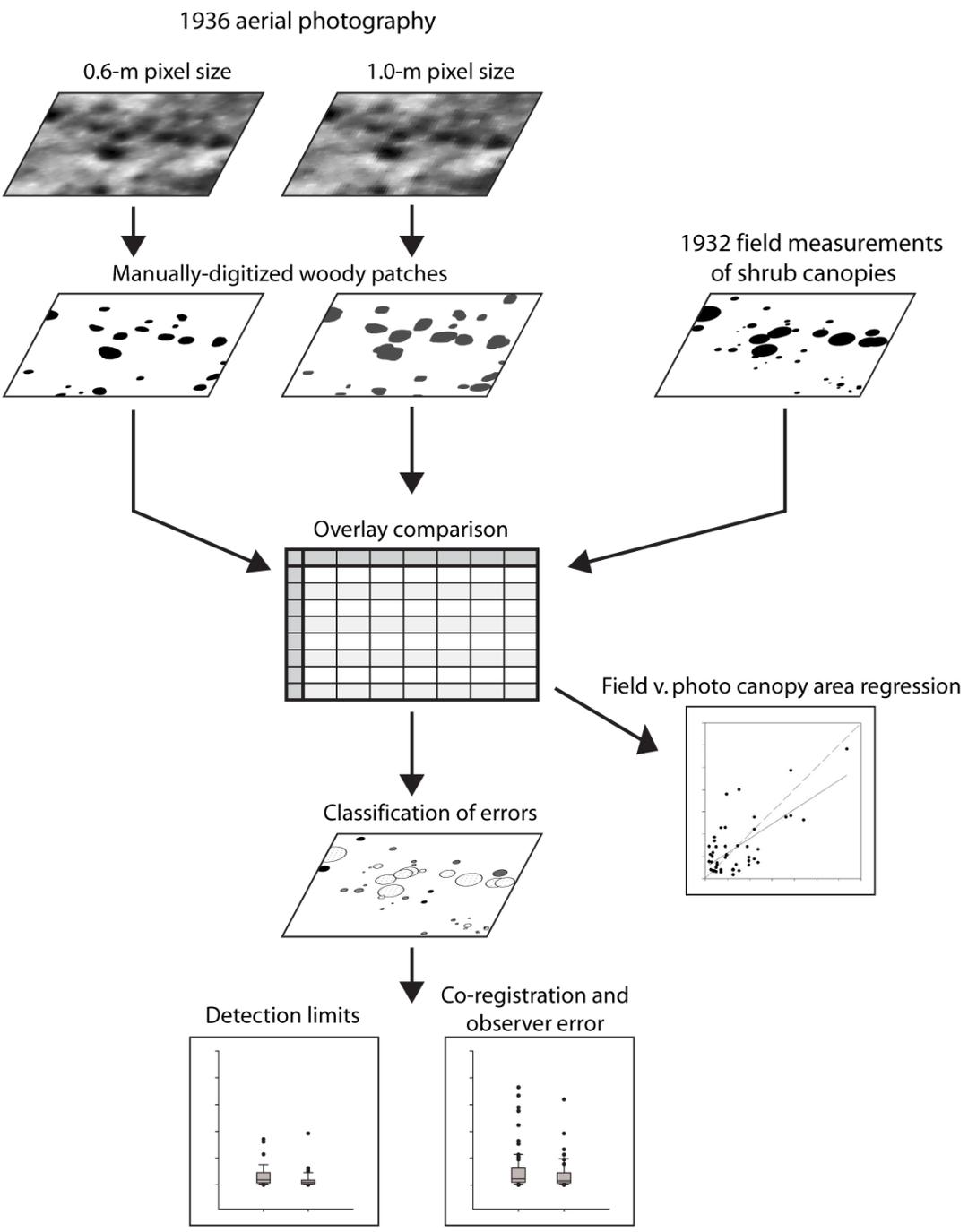


Fig. 2

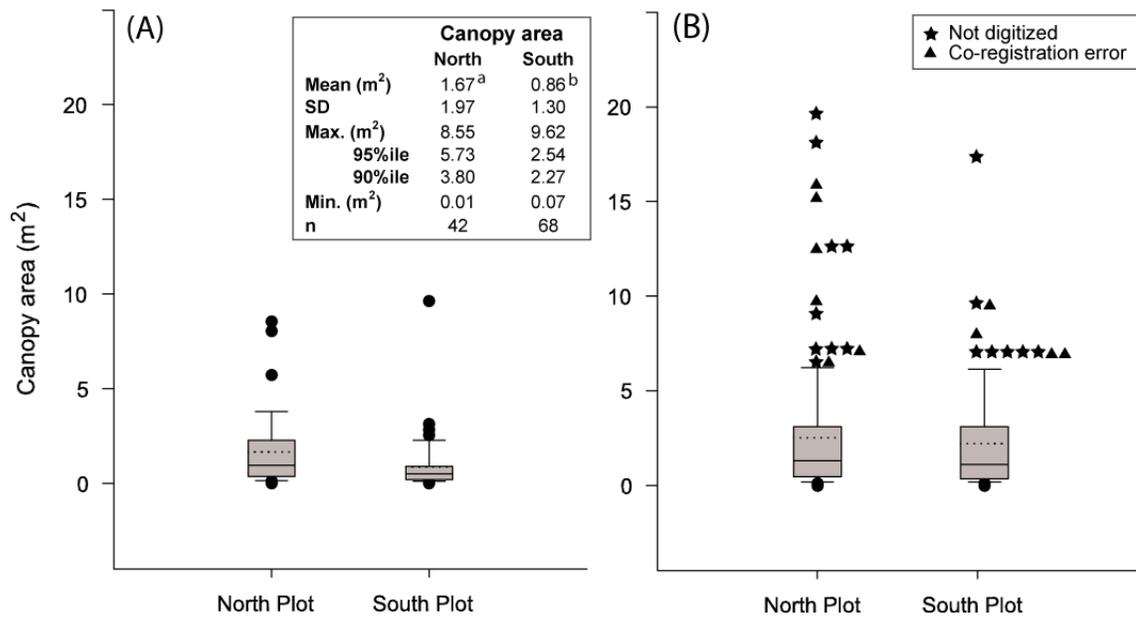


Fig. 3

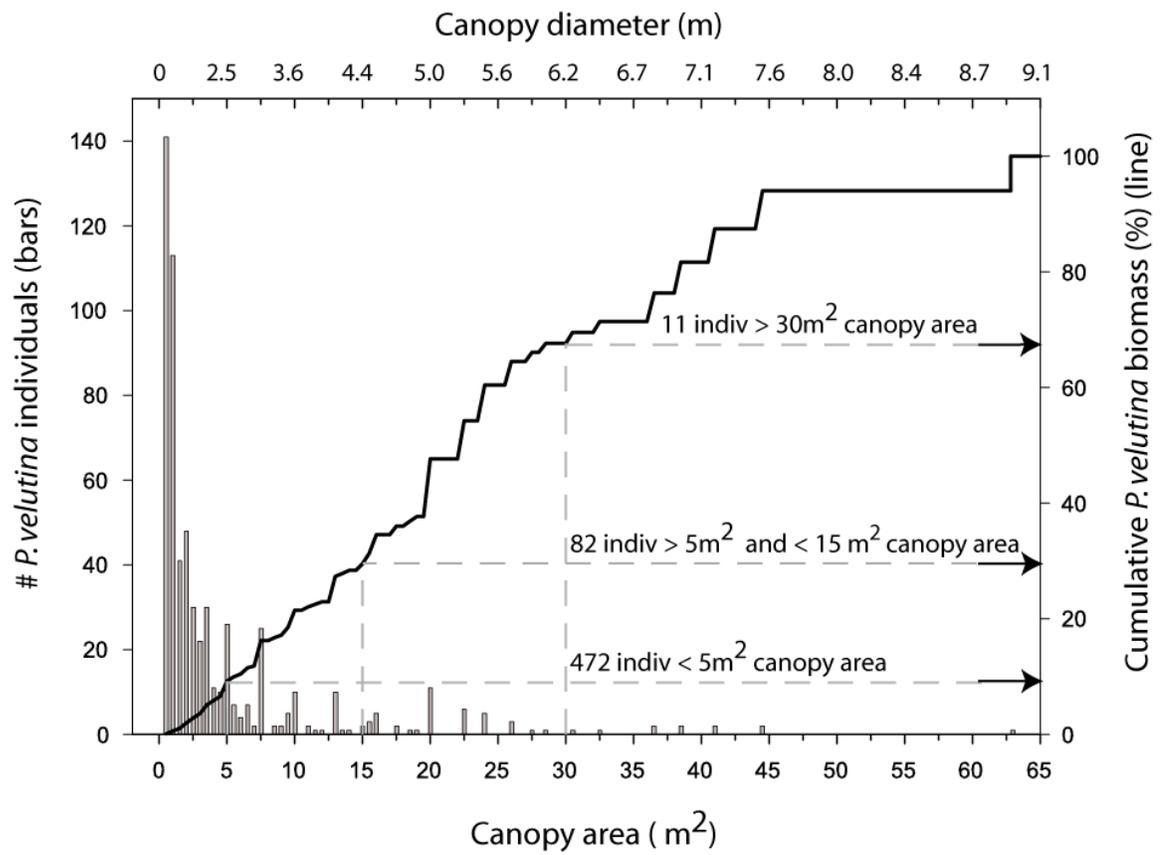


Fig. 4

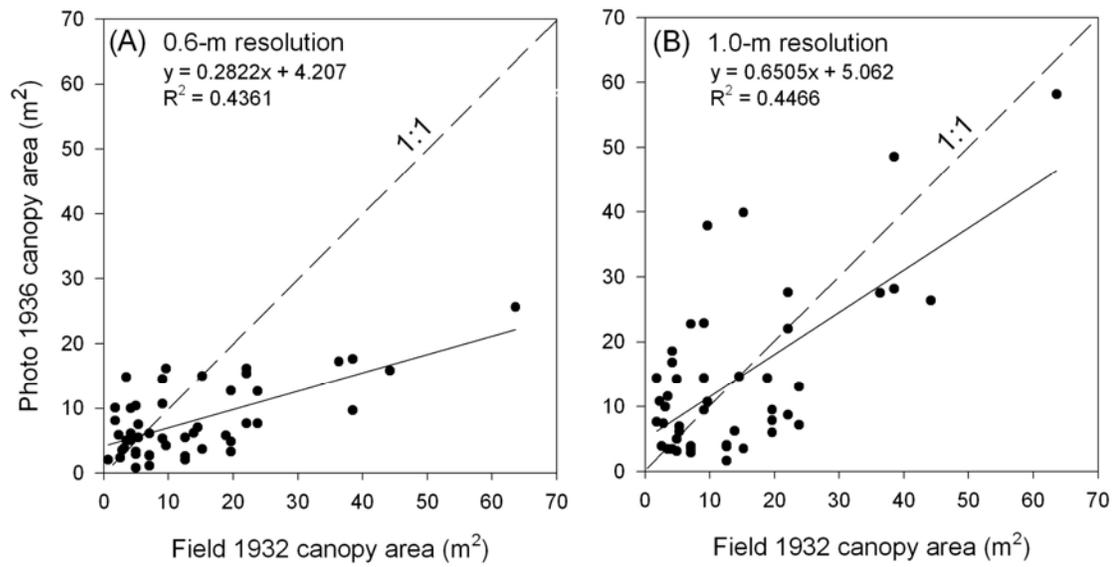


Fig. 5

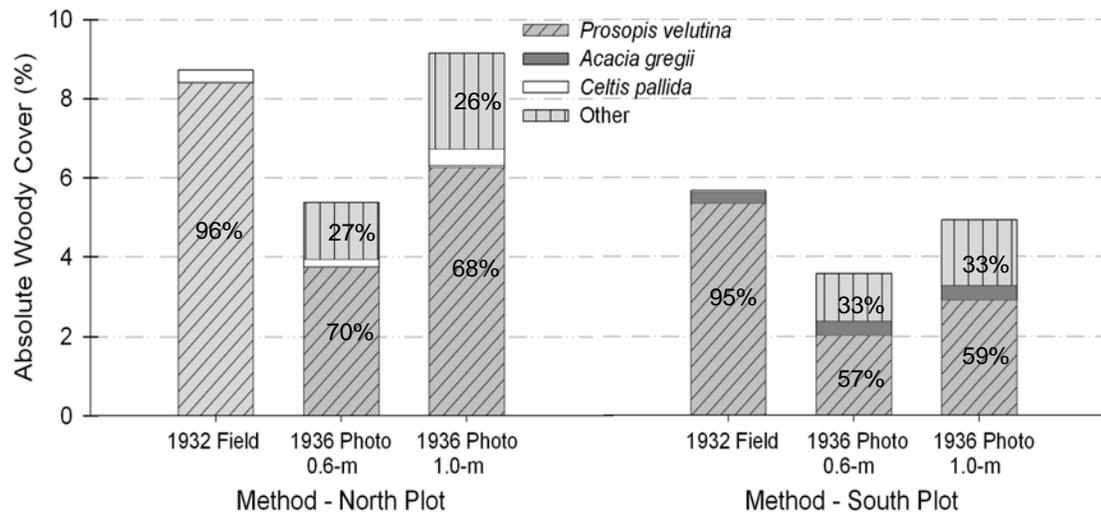


Fig. 6

APPENDIX C

**DISTURBANCE, SPACE, AND TIME: LONG-TERM MESQUITE (*PROSOPIS
VELUTINA*) DYNAMICS IN SONORAN DESERT GRASSLANDS (1932 – 2006)**

DAWN M. BROWNING, STEVEN R. ARCHER, D. PHILLIP GUERTIN

(To Be Submitted to Ecological Applications)

Abstract:

Woody plants have increased in abundance in grasslands and savannas worldwide. Livestock grazing is widely regarded as a key factor in the shrub encroachment process, although most evidence is circumstantial. Mapping of velvet mesquite (*Prosopis velutina*) plants in and out of livestock exclosures constructed in 1932 on the Santa Rita Experimental Range in southeastern Arizona and re-mapping in 1948 and 2006 afforded us the opportunity to quantify effects of livestock grazing on *P. velutina* population structure, cover, density, and biomass over 74 years in Sonoran desert grasslands. In 1932, *P. velutina* cover and density was comparable on grazed (12% and 173-plants ha⁻¹) and recently protected sites (8.4% and 203-plants ha⁻¹). By 1948 *P. velutina* cover had increased to ca. 18% on both sites, but mean plant density on the protected plot increased 300% (603-ha⁻¹) and was nearly 2X that on the grazed plot (318-ha⁻¹). This primarily reflected greater recruitment of new plants on the protected area (513 plants ha⁻¹) relative to the grazed area (155 plants ha⁻¹), as mortality was equally low (~ 0.06%) on both plots. Data suggest maximum *P. velutina* cover may be dynamically stable at ca 30%. Aerial herbicide applications in 1965/1966 are said to have reduced cover 90% across the study area. By 2006, total aboveground *P. velutina* carbon mass was comparable on grazed and protected areas (2.1-Mg ha⁻¹), but cover and density on the protected area (21.9% and 960-ha⁻¹) significantly exceeding that on the grazed area (15.4% and 433-ha⁻¹). Spatial autocorrelation in *P. velutina* density did not deviate from random over 74 years on the grazed area, whereas patterns on the protected area became increasingly positive.

Protection from livestock facilitated the formation of dense shrub clusters and open areas generating high spatial heterogeneity. Collectively, results are counter to the common generalization that livestock grazing promotes woody plant encroachment. Indeed, in this semi-desert grassland ecosystem, livestock grazing retarded rather than promoted woody encroachment over 74 years. Results from our long-term study are in accordance with short-term seedling establishment studies with leguminous shrubs in other systems and indirectly point to the critical role of fire as a proximate factor regulating shrub establishment and stand development in grasslands.

Introduction:

Land use legacies influence the contemporary structure and distribution of vegetation. Disregard for historic land uses can place short-term studies in the ‘invisible present,’ possibly yielding misleading conclusions (Magnuson 1990, Weltzin et al. 1997). Interpretations of current spatial patterns and linkages to processes that generate them are informed by knowledge of past land management activities (Peters and Havstad 2006). Livestock grazing, the most geographically extensive form of land use worldwide (Asner et al. 2004), can directly or indirectly cause changes that persist for decades (Archer 1995). In this context, footprints of historic land uses imposed upon grasslands and savannas (hereafter “rangelands”) and their effects on ecosystem function are especially relevant to management activities associated with livestock production and agricultural practices.

A shift from herbaceous to woody plant domination has occurred in rangelands worldwide (Archer 1995) with ramifications for nutrient cycling (e.g., Wessman et al. 2004), primary production (e.g., Knapp et al. 2008), soil erosion (Schlesinger et al. 1990), and sustainable land use practices (Lambin et al. 2007). The proliferation of trees and shrubs in rangelands has been attributed to a number of interacting factors, including changes in herbivory, climate, fire regimes and atmospheric CO₂ enrichment (Archer 1994, Archer et al. 1995, Van Auken 2000). Livestock grazing is widely regarded a driver in the process of woody plant encroachment (Bahre 1991, Skarpe 1992, Archer 1996); however, evidence in support of this assumption is mixed (Scholes and Archer

1997, Sankaran et al. 2008). Interactions between grazing, climate, and fire may be promoted or constrained by the underlying geomorphic template and land use history, thereby complicating the task of disentangling the contributions of individual drivers (Archer 1996, Fuhlendorf and Smeins 1997, House et al. 2003, Sankaran et al. 2005).

Direct assessments of livestock grazing as a driver of increases in woody plant abundance are hampered by challenges that span spatial and temporal scales and availability of requisite data. First, information needed to assess grazing impacts [stocking density, distribution, seasonality and duration (e.g., rotational versus year-long grazing)] is seldom available. Second, livestock grazing influences on ecosystem processes are strongly mediated by spatial, seasonal and interannual variation in precipitation; and such climate records often do not exist. Third, long-term experimental manipulations or observations are required to elucidate grazing treatment effects on vegetation (Mashiri et al. 2008). Fourth, grazing alters processes determining patterns of woody vegetation at multiple spatial scales. Livestock alter fine-scale patterns of vegetation distribution via seed dispersal (Janzen 1984, Brown and Archer 1989), trampling, and the selective utilization of plants (Heitschmidt and Stuth 1991) and broad-scale fire disturbance by modifying fine fuel biomass and continuity (i.e., herbaceous ground cover) (Senft et al. 1987, Archer 1994, Fuhlendorf et al. 2008). Finally, the longevity of many woody species requires a multi-decadal perspective that captures the net outcome of climate X grazing interactions on recruitment, mortality and stand development.

The shift from herbaceous to woody plant domination in rangelands constitutes a potentially significant, but highly uncertain component of the North American terrestrial carbon budget (Houghton et al. 1999, Pacala et al. 2001). Recent efforts to understand the effects of land use on global change highlight the need to quantify the effects of livestock grazing on biomass and carbon pools across broad spatial extents (special issue of *Rangelands* 2008:30(3), Asner and Archer *In Press*). Rangelands are geographically extensive, covering ca. 40% of the global land surface (Bailey 1996), and are characterized by high spatial heterogeneity. As such, quantifying aboveground biomass at broad spatial scales is a major challenge (Gifford and Howden 2001, Lu 2006). Furthermore, projections of future biomass changes in vegetation require knowledge of plant population structure (Hurt et al. 2002) that cannot be generated by traditional broad-based assessments of percent cover. Long-term perspectives on plant demographics afford the historical context required to enhance understanding of the effects of livestock grazing on woody plant dynamics, spatial patterns in woody plant recruitment, stand development, and biomass loss and/or accrual (Asner and Archer *In Press*).

The spatial configuration of woody plants influences the distribution of water and soil nutrients (Ludwig et al. 1997, Huxman et al. 2005, Ludwig et al. 2005, de Knecht et al. 2008). Patterns of woody plant distribution in rangelands are important to the spread of disturbance and soil loss due to erosion, as well as of practical importance to livestock management with regard to animal handling and time spent foraging (Archer 1994). Spatial context is inextricably linked to dispersal, recruitment, competition, and

disturbance (Moloney and Jeltsch 2008); as such, spatial context plays an important role in the process of woody plant encroachment. Ecological processes act at multiple spatial scales, highlighting the need to assess patterns at local as well as broad scales of analysis; realistic depictions of change across complex landscapes necessitate cross-scale linkages (Hampe et al. 2008). In this manner, spatial metrics (e.g., Moran's I) may be more sensitive to treatment effects than broad-scale measures of vegetation abundance (e.g., percent cover). Measures of autocorrelation structure characterize spatial associations related to dispersal and recruitment and depict spatial relationships at local and global spatial scales. Statistical assessments and predictive models incorporating the functional role of spatial structure are apt to capture previously unexplained variance and improve capabilities to forecast woody stand dynamics and carbon storage potential in rangelands.

In exploring the spatial patterns of vegetation response to livestock grazing, herbaceous cover has been emphasized (see Adler et al. 2001). The few studies that have quantified spatial patterns of woody cover change have relied on aerial photography; spatially explicit plant-centered perspectives are rare. Goslee et al. (2003) found that patterns of shrub patch cover shifted from clumped (or aggregated) to randomly distributed (no distinct pattern) to regular (or dispersed) over time in the Chihuahuan Desert. Seifan and Kadmon (2006) attempted to use aerial photography to determine if livestock grazing would promote a random pattern of shrub distribution. With lacunarity analysis, they found no pattern in shrub patch distribution on heavily grazed areas while lightly grazed areas exhibited some degree of clustering in distribution. However, the resolution of the imagery was such that they could not

account for young (small) shrubs nor distinguish among individuals growing in close proximity. Thus, their assessments of spatial pattern disregard ecological processes (e.g., recruitment and mortality) that are key to their conceptual model; the pattern is limited to patches rather than individuals. We circumvent this limitation to evaluate spatial patterns in woody plant density on plots grazed and those protected from livestock for velvet mesquite (*Prosopis velutina* var Woot.), a shrub that has extensively invaded semi-desert grasslands in the southwestern U.S.A., begins in 1932 with historic perspectives in southeastern Arizona.

There has been long-standing interest in understanding the influence of livestock grazing on woody plants as well as on herbaceous biomass. As part of this effort, a livestock exclosure experiment was initiated in 1932 on the Santa Rita Experimental Range in southeastern Arizona by W. McGinnies to monitor the effects of herbivory by livestock and lagomorphs with an exhaustive field survey of shrubs and cacti. Glendening (1952) replicated field measurements of shrubs and mapping endeavors in 1948 and found no discernable effect of grazing on percent cover for *P. velutina* after 16 years of protection from livestock or lagomorphs. Furthermore, he proposed that *P. velutina* cover would stabilize at 30%. We extended this work by re-measuring a portion of these plots in 2006 and quantified changes in *P. velutina* density from 1932, 1948 and 2006 in a spatial context.

Our objectives were to conduct an exhaustive census of woody plants on a long-term plot spanning grazed and ungrazed treatments and to quantify effects of livestock grazing from 1932 to 2006 on changes in biomass, canopy cover, density, and population

structure of *P. velutina*. We consider changes across time and space by supplementing conventional statistical procedures with an evaluation of autocorrelation structure in broad (global) and fine (local) spatial contexts. We sought to answer the following questions: Does livestock grazing (a) promote increases in *P. velutina* density and cover, and (b) influence patterns of spatial autocorrelation? Specifically, does livestock grazing result in a random distribution of shrubs?, and (c) How do changes in population structure translate to changes in aboveground biomass?

Methods:

Study site

The study was conducted on the Santa Rita Experimental Range (SRER) in southeastern Arizona, USA (31.81386° N, -110.8886° W, Fig. 1A), where increases in *P. velutina* are known to have occurred since 1900 (McClaran 2003). Situated on an alluvial fan terrace on the western flank of the Santa Rita Mountains, the physiognomy on the SRER ranges from desert scrub at lower elevations (875-m) to oak (*Quercus* spp.) savanna/woodlands at the highest elevations (1,400-m) (McClaran 2003). Annual precipitation is bimodal with a pronounced peak in late summer (July-September monsoon) and a lesser peak in winter; mean annual precipitation is positively associated with elevation, ranging from 296-mm at lower elevations (866-m) to 498-mm at upper elevations (1372-m). See McClaran et al. (2003) and <http://ag.arizona.edu/srer> for additional details on climate, livestock management, soils and vegetation.

Prior to its establishment in 1902, the SRER was subjected to heavy, year-long, unregulated cattle grazing. Cattle were removed shortly after the establishment of the SRER and then re-introduced in 1916. Year-long grazing was practiced from 1916 until 1972 with steadily decreasing stocking rates from a maximum of 0.17 animal unit years per ha in 1918 (Ruyle 2003). A rotational grazing system (Martin and Severson 1988, Mashiri et al. 2008) was implemented in 1972 and maintained through the 2006 census date (Fig. 1D).

This study capitalizes on two 1.8-ha plots (440-m X 40-m, 510646-m E, 3519765-m N) established in 1932 by W. McGinnies to evaluate the effects of herbivory on woody plants and cacti on a sandy loam upland site [fine, mixed, superactive, thermic Ustic Paleargids; (Breckenfeld and Robinett 2003)] at 1,100-m elevation (Fig. 1C). Mean annual precipitation (1922-2007; derived from the Rodent Station rain gauge situated 330-m from the study site) was 354-mm with an average summer (June – September) precipitation of 207-mm (Standard Deviation, SD = 72.9) and an average winter precipitation (October – May) of 147-mm (SD = 69.0). Ten years prior to the 1932 census was a dry period with eight years receiving below-average rainfall. The period from 1932 to 1948 was marked by consistent below-average rainfall, whereas the 58 years between 1948 and 2006 were characterized by increased variability in seasonal precipitation patterns with periods of consistently above-average rainfall (1980s) interspersed with average and dry periods (2000-2005) (Browning et al. 2008).

Plots were gridded with permanent re-bars at 10-m intervals and subdivided into three treatments: (1) protected from lagomorphs (jackrabbits, *Lepus californica eremicus*

Allen and *L. alleni alleni* Mearns; and cottontails, *Sylvilagus auduboni arizonae* Allen) and cattle, (2) protected from cattle, and (3) open to cattle and lagomorphs. All plots were open to small mammals [e.g., Merriam (*Dipodomys merriami merriami* Mearns) and Bannertail (*D. spectabilis spectabilis* Merriam) kangaroo rats] which are known to cache *P. velutina* seeds (Reynolds and Glendening 1949). Lagomorph exclosures were not maintained after 1948.

In May 2006, we repeated field measurements taken in 1932 and 1948 (described in next section). High shrub densities in 2006 limited this endeavor to a 200-m X 40-m portion of the North plot (Fig. 1C) centered on the livestock exclosure treatment boundary. The 0.8-ha area surveyed in 2006 comprised a 100-m X 40-m (0.4-ha) area open to lagomorphs and livestock since 1916 (hereafter, “grazed plot”) and an identical sized area closed to livestock since 1932 and closed from 1932 to 1948, but open to lagomorphs after 1948 (hereafter, “protected plot”). Analyses of spatial autocorrelation require contiguous coverage for variables of interest (Fortin and Dale 2005).

Incorporating spatial analyses in our research objectives precluded random sampling of subplots within the two plots established in 1932. Discontinuity of the lagomorph-protected treatment (post-1948) hindered long-term assessment of the effects of browsing by lagomorphs on *P. velutina* stand structure. We tested for differences in *P. velutina* density (following 16 years of protection) between the 20-m X 20-m subplots protected from lagomorphs and cattle and those protected from cattle only. *P. velutina* densities in 1948 were comparable on 20-m X 20-m subplots protected from lagomorphs and livestock ($n = 5$, mean \pm standard error, 27.4 ± 7.5) and subplots protected only from

livestock ($n = 5$, 20.8 ± 4.5) (ANOVA $F = 0.38$, $df = 1, 8$, $p = 0.555$). We therefore pooled these treatments (i.e., protected from lagomorphs and livestock with protected from livestock only) for all parametric treatment comparisons.

In May 1964 and 1965, a 161-ha area encompassing the McGinnies plots was treated with an aerial herbicide (2,4,5-Trichlorophenoxyacetic acid) as part of a study aimed at managing *P. velutina* cover (Martin and Ward 1966). Quantitative reports of herbicide efficacy (e.g., mortality, reductions in crown cover for individual plants) are not available; however, Martin and Ward (1966) reported a crown recovery of 11% one season after the treatment. Knowledge of this aspect of site history thus afforded the opportunity to determine if grazing history has influenced recovery from this disturbance.

Field data collection

The canopy diameter of all woody plants [primarily *P. velutina*, with some *Celtis pallida* and *Acacia greggii*] and cacti (*Opuntia* spp)] was measured by W. McGinnies to the nearest 0.1-m in 1932. Plants were re-measured in 1948 and their locations were mapped using a telescopic alidade and plane table (Glendening 1952). In 2006, re-bars denoting the plot corners and 10-m X 10-m cells were geo-coded with a Leica GS20 Global Positioning System with WAAS (Wide Area Augmentation System, with minimum 0.5-m positional accuracy). In May 2006, we replicated historic field measurements for all woody plants within the 200-m X 40-m subset of the North plot and recorded Universe Trans Mercator (UTM) coordinates at the bole of each *P. velutina*

plant. UTM coordinates were translated to cartesian coordinate space using an affine transformation and ten control points (RMS error = 0.244-m).

GIS data processing

Scaled, hand-drawn maps from 1932 and 1948 acquired from the SRER Archives were scanned (Epson 836XL scanner). Maps were spatially registered with ArcMap (v. 9.0, ESRI, Inc.) to a grid (defined using 10-m X 10-m cells) generated in AutoCad. Point files for 1932 and 1948 plant locations were created within a geographic information system (GIS) database by digitizing plant locations demarcated on the spatially referenced field maps. Unique identifiers were assigned to each plant and field measurements were compiled and linked to point file attribute tables. Field canopy diameter measurements were used to compute canopy area as that of a circle. Overlapping canopy boundaries were dissolved in ArcMap to generate projected canopy cover.

P. velutina cover and density

Percent cover and plant density were calculated for 20-m X 20-m non-overlapping subplots ($n = 10$ grazed and $n = 10$ protected) following protocols of Glendening (1952). This was done to permit comparison of our 2006 data (within the 0.8-ha subset) to those previously reported. With the exception of reported mean cover and density from Glendening (1952), repeated measures were confined to the 200-m X 40-m plot (Fig. 1C). Variables were assessed for normality and statistical comparisons were conducted with SAS (v. 9.1, SAS Institute 2002). Changes in *P. velutina* cover and

plant density were analyzed using repeated measures analysis of variance (ANOVA). Normality assumptions prior to repeated measures ANOVA were evaluated with studentized residuals. Paired t-tests were used to evaluate changes in percent cover and patch density in each time step.

To evaluate Glendening's (1952) prediction that landscapes would stabilize at 30% cover, we computed the probability of *P. velutina* cover increasing for a given initial cover condition for the 1932 to 1948 and 1948 to 2006 periods using 20-m X 20-m subplots. Given the low sample size ($n = 10$ subplots per treatment per time period) and similarities in transition outcomes for grazed and protected subplots, data were pooled across treatments and time periods, yielding 40 transitions.

To distinguish effects of the 1965/66 aerial herbicide on woody plant cover, we capitalized on field-measured estimates of cover from study plots that were not treated with the 1965/66 herbicide. In 2004, we established 30-m X 30-m plots to validate woody cover estimates derived from aerial photography as part of another study. Study plots were situated 1.2-km from the study McGinnies plots in this study on same soil, and were subjected to the same grazing practices as the McGinnies plots open to livestock grazing with no known brush management history (Browning et al. 2008). We measured canopy area for all woody plant patches; percent cover was determined by dividing total canopy area by the area of the plot. Mean cover from the three plots occurring on similar soils (i.e., sandy loam uplands) was treated as a control for the 1965/66 herbicide treatment.

Population structure and P. velutina biomass

Canopy size distributions were evaluated using paired Kolmogorov-Smirnoff (K-S) tests (Daniel 1978) and mean *P. velutina* canopy sizes were compared using ANOVA. A relationship between natural log-transformed *P. velutina* canopy area and aboveground biomass developed for this site [$R^2 = 0.97$, $n = 32$ trees; (Browning et al. 2008)] was used to estimate *P. velutina* biomass in 1932, 1948 and 2006. Effects of livestock grazing on aboveground *P. velutina* biomass were quantified at two scales: (1) mean plant mass within each 0.4-ha treatment plot, and (2) plot-level *P. velutina* biomass by summing values across all plants in each 0.4-ha grazing treatment. To examine landscape biomass in the context of *P. velutina* stand structure, we present contributions to total biomass by *P. velutina* canopy size class.

Spatial autocorrelation structure

Data exhibiting spatial autocorrelation are not independent, and thus violate a key assumption of common statistical methods (Legendre 1993). Correlated observations reduce the number of degrees of freedom; and positively correlated data decrease within group variance, thereby increasing the chance of Type 1 error (Cliff and Ord 1981). The spatial autocorrelation structure of *P. velutina* plant density and percent cover was evaluated to: (1) test the assumption of independent observations for analyses involving the 20-m X 20-m subplots (or cells) and (2) examine the effect of livestock grazing on patchiness and spatial arrangement of woody vegetation. We selected 5-m X 5-m cells to characterize spatial heterogeneity in *P. velutina* density because the cell size

corresponded roughly to mean canopy size (Fig. 4, inset) and represented patterns of *P. velutina* density masked with larger cell sizes. An indicator of spatial autocorrelation, global Moran's I were determined using GeoDa (v.0.9.5) (Anselin et al. 2006) for plots grazed by livestock since 1916 and plots protected from livestock for 74 years. We quantified first-order correlations (single lag, nearest neighbor) for each 5-m X 5-m cell with its eight neighbors.

Ecological processes act at multiple spatial scales and prompt consideration of spatial pattern at multiple levels. Local spatial statistics represent spatial pattern within neighborhoods, as a means of depicting spatial heterogeneity that is averaged in a global metric (Getis and Ord 1992). We decomposed the global index of spatial association (Moran's I) into contributions from local neighborhoods using Local Indicator of Spatial Association (LISA) (Anselin 1995), which quantifies the extent to which cells are similar to or different from their neighbors. In addition, LISA values illustrate the local deviation and influence of each cell on the global measure of spatial association (Anselin 1995), thereby signifying how local patterns contribute to the global statistic (Wagner and Fortin 2005). In our case, neighboring cells of similarly high *P. velutina* density (high - high) could result from short-range seed dispersal or favorable microsite conditions, whereas negative spatial associations (high - low and low - high) may reflect biotic interactions (i.e., competition) (Fortin and Gurevitch 2001). Significant deviations from a random pattern of association relative to the mean density were determined using 999 random permutations of Moran's I for grazing and year comparisons at $\alpha = 0.001$.

Results:*P. velutina* cover and density

Mean *P. velutina* density and cover were comparable within 20-m X 20-m subplots on grazed and protected plots in 1932; and density and cover estimates for the 0.8-ha plot corresponded to those reported for the entire 3.6-ha area in 1932 and 1948 (Fig. 2, Glendening 1952). Cover increased between 1932 and 2006 but was not significantly related to livestock grazing ($F = 0.1$, $df = 1, 18$, $p = 0.747$, Fig. 2A; grazing X year, $F = 2.9$, $df = 2, 17$, $p = 0.085$). Cover increased significantly between 1932 and 1948 for both protected ($t = -4.98$, $df = 9$, $p = 0.001$) and grazed ($t = -3.41$, $df = 9$, $p = 0.008$) plots; and values in 2006 were statistically comparable to those in 1948 ($t = 0.85$, $df = 9$, $p = 0.417$ for grazed and $t = -1.05$, $df = 9$, $p = 0.323$ for protected) following the herbicide applications in 1964/65. By 2006, *P. velutina* cover was significantly higher on the protected plot. Percent cover from 30-m X 30-m plots (as part of another study) not treated with the 1965/66 herbicide was considerably higher (mean \pm standard error, $35.6 \pm 2.0\%$) than cover for the treated grazed plot ($15.4 \pm 2.3\%$), reflecting a legacy effect and net reduction in *P. velutina* cover 40 years after the herbicide treatment (Fig 2A).

P. velutina density increased over both periods, more so on the protected plots than on the grazed plots (grazing X year $F = 4.3$, $df = 2, 17$, $p = 0.031$, Fig. 2B). The interaction reflects statistically significant increases in plant density between 1932 and 1948 ($t = -4.41$, $df = 9$, $p = 0.002$) and 1948 and 2006 ($t = -3.99$, $df = 9$, $p = 0.003$) on the protected plot, whereas significant increases in plant density occurred only from 1932 to

1948 ($t = -3.82$ $df = 9$, $p = 0.004$) on the grazed plot. This difference in treatment response for *P. velutina* density is similarly expressed by significantly higher mean density on the protected plot in 1948 and 2006 using Tukey's Studentized Range test, $\alpha = 0.05$ (Fig. 2B).

Changes in *P. velutina* cover were spatially heterogeneous over the 74-yr period (Fig. 3), but overall probabilities of cover increase at the scale of 20-m X 20-m subplots on grazed and protected plots were similar. The probability of *P. velutina* cover increasing was highest (0.8 to 1.0) when total cover was < 25% and declined to 0.5 when cover was 26-30% (Table 1). When cover was > 30% the probability of increase was 0.0.

P. velutina population structure

Between 1932 and 1948 more *P. velutina* plants appeared on the 0.4-ha protected plot ($n = 205$, 513 plants ha^{-1}) than on the 0.4-ha grazed plot ($n = 62$, 155 plants ha^{-1}). Mortality over these 16 years was low on both protected (0.07%) and grazed plots (0.06%) with no significant difference in mean canopy radius of plants that died on grazed [0.75 (0.5)-m] and protected [1.39 (0.5)-m] plots ($t=0.87$, $df=8$, $p=0.409$). The 58-yr period from 1948 to 2006 was marked by sustained high levels of recruitment on both plots (Fig. 3).

Canopy size distributions were significantly different on grazed and protected plots when the study was initiated [Fig. 4A; asymptotic Kolmogorov-Smirnov ($K-S_a$) = 1.81, $p = 0.003$]. Size-class distribution differences in 1948 ($K-S_a = 1.5$, $p = 0.024$) reflect greater recruitment between 1932 and 1948 on the protected plot ($K-S_a = 2.28$, $p <$

0.0001) than on the grazed plot ($K-S_a = 1.29$, $p = 0.071$, Fig. 4B). Canopy size distributions on both plots were further skewed toward smaller plants between 1948 and 2006 ($K-S_a = 2.14$, $p < 0.0002$ for grazed and $K-S_a = 3.42$, $p < 0.0001$ for protected), presumably a combination of the 1965/66 herbicide application. Although the number of plants was substantially higher on the protected plot than on the grazed plot in 2006, size class distributions were statistically comparable ($K-S_a = 0.989$, $p = 0.281$, Fig. 4C).

Mean *P. velutina* canopy sizes on grazed and protected plots were statistically comparable when the study was initiated in 1932 (Inset, Fig. 4A). Owing to the establishment of numerous small plants, mean plant canopy area declined between 1932 and 1948, more so on protected plots than on grazed plots (Fig. 4B). This trend continued through 2006 (Fig. 4C), by which time, the variation in mean plant canopy area was markedly reduced, perhaps reflecting effects of the 1964/65 herbicide application.

P. velutina aboveground biomass

Total *P. velutina* aboveground biomass increased from 1932 to 1948 with a greater net increase in biomass on the protected plot, due to growth of the largest plants (Fig. 5B). The decline in biomass from 1948 to 2006 on both plots was presumably the result of the 1964/65 herbicide treatment. It appears that herbicide-induced loss of biomass from the largest trees more than offset increases in biomass associated with the appearance of new plants (Figs. 3 and 5B). Seventy-four years after the grazing contrast was established and forty years after the aerial herbicide was applied, total woody aboveground biomass converged at approximately 4.5-Mg ha^{-1} regardless of grazing

history. By 2006, all plants contributing to *P. velutina* biomass had canopies $< 50\text{-m}^2$ in size. Mean aboveground biomass on a per plant basis was not different between 0.4-ha grazed and protected plots in 1932 ($F = 0.97$, $df = 1, 149$, $p = 0.326$) and 1948 ($F = 0.83$, $df = 1, 366$, $p = 0.364$), but did diverge by 2006 ($F = 7.99$, $df = 1, 559$, $p = 0.005$). Mean plant mass was relatively stable between 1932 and 1948. Substantial reductions in the mean and standard error plant biomass occurred by 2006 (Fig. 5B inset).

Spatial autocorrelation structure

P. velutina cover and density on grazed and protected plots were not spatially autocorrelated within 20-m X 20-m subplots (Table 2). Thus, the assumption of independent observations underlying repeated measures ANOVA was not violated. Scatter plots for plant density within 5-m X 5-m subplots, from which Global Moran's I values were generated, indicated increasing variability in association over time (Fig. 6). There was no distinct pattern of spatial association on the grazed plot relative to what would be expected from a random arrangement of density values ($p = 0.061$ to 0.355). In contrast, patterns of association between neighboring 5-m X 5-m cells on the protected plot revealed localized formation of shrub clusters (high density cells surrounded by high density cells, denoted 'High – High' in Figs. 6 and 7) more so than open areas (low density cells surrounded by low density cells, denoted 'Low – Low' in Figs. 6 and 7).

Decomposition of the global Moran's I for plant density within 5-m X 5-m subplots illustrated different dynamics in spatial association on grazed and protected plots (Fig. 7). Pre-treatment patterns of association (low – low and high – high) existed on

portions of the plot slated for livestock and lagomorph exclusion. The protected plot exhibited higher spatial variability in plant density (Figs. 3 and 7) and reflected nonstationarity or spatial inconsistency in mean *P. velutina* density. Neighbor associations indicative of competitive interactions (high – low and low – high configurations) were not strong, although they occurred on both grazed and ungrazed plots. To illustrate linkages between global and local measures of association, two 5-m X 5-m subplots that deviated from mean density most strongly (on the protected plot) are circled in Fig. 6 and darker in color in Fig. 7.

Discussion:

Fluctuations in woody plant cover, density, and biomass from 1932 to 2006 were dynamic across space and time. In this study, we documented long-term effects of grazing by livestock on *P. velutina* stand structure at multiple spatial scales. First, we presented biomass from both plant and plot perspectives to understand carbon storage potential. Second, we evaluated changes in *P. velutina* cover and density within 20-m x 20-m subplots and supplemented this by considering spatial patterns in density using 5-m x 5-m subplots. *P. velutina* stand structure and spatial patterns were more sensitive to livestock grazing than were estimates of canopy cover.

Brush management has a long history in rangelands (Scifres 1980, Bovey 2001), posing important consequences for land cover change; yet it is often overlooked (Asner et al. 2003). This may be due to the paucity of spatially explicit records of treatment history, but legacy effects on cover, biomass, and vegetation structure should not be

underestimated. In this study, temporal interpretation of changes in *P. velutina* cover, biomass, and stand structure from 1948 to 2006 are confounded by the herbicide treatment, although interpretations from 1932 to 1948 are unaffected. However, the grazing contrast is persistent and permits comparison of treatment effects over time. Although we lack records on the effectiveness of herbicide treatments for our study site, there is evidence of long-term effects of the same herbicide on *P. velutina* and herbaceous cover at slightly higher elevation (Cable 1976). Cable (1976) reported 50% mortality and reduction of 90% in crown cover for individual *P. velutina* plants; stand recovery was slow. Twenty years after treatment shrub densities (533 shrubs/ha) approached pre-treatment levels (556 shrubs/ha) (Cable 1976). These data are the best available evidence that cover in 1965/66 was reduced 90%. With no indication that pre-treatment vegetation conditions would influence the response to disturbance, we focus our attention to interpretations of livestock grazing effects on stand dynamics, biomass, and spatial pattern.

Grazing effects on P. velutina stand dynamics

Our results correspond with those of Bakker and Moore (2007) in northern Arizona ponderosa pine forests in that removal of livestock resulted in enhanced recruitment and subsequent increases in cover and density of woody plants on ungrazed plots. We identified a number of possible mechanisms to explain how livestock might affect woody plant dynamics and stand structure while recognizing future research is required to identify relative importance of proposed mechanisms. First, the importance

of livestock as dispersal vectors may be diminished once seed-bearing plants are distributed across the landscape (Glendening 1952). As such, a positive feedback in cluster development is initiated with seedlings more likely to establish near the parent plant. Second, with an adequate seed source, the presence of livestock may negatively influence seedling establishment by browsing and/or trampling (Huntly 1991). Third, survival of plants present when the study was initiated may have been enhanced by removing livestock. All mechanisms could be invoked to explain observed increases in density and clustering on the protected plot; however, directed field experiments and further analysis are required. Decreases in woody plant cover and density due to livestock grazing coincide with observed changes in arid and semi-arid ecosystems (Cheal 1993, Mengistu et al. 2005), yet are counter to other studies reporting increases in woody cover and density attributed to livestock grazing in rangelands (Madany and West 1983, Skarpe 1990, Roques et al. 2001).

The 74-yr field perspective revealed changes that were counter to expectation. Long-term data are required to capture woody plant responses to livestock grazing manipulations (Mashiri et al. 2008); and it is important to recognize that sampling frequency contributes to plausible interpretation of long-term data. The 58-year lag between second and third field campaigns precludes determination of timing of *P. velutina* establishment, but does provide a reference for changes that occurred over decadal time frames. Glendening (1952) noted the existence of a viable seed bank and seed-bearing trees on this site in 1932. Our results, in conjunction with Glendening (1952) agree with others that have observed *Prosopis* spp. had already established a

foothold in the grassy matrix prior to 1932 (Archer et al. 1988, Goslee et al. 2003, Bestelmeyer et al. 2006).

In arid and semi-arid ecosystems, annual precipitation imposes an abiotic constraint on maximum woody cover (Sankaran et al. 2005), but disturbance, soils, and biotic interactions prevent realization of this potential. Forty years after the herbicide disturbance reduced *P. velutina* cover 90%, protection from livestock resulted in significantly higher woody cover. Mechanisms driving the increase in cover on protected subplots following the herbicide are unclear, but are likely a combination of those posed above. Persistence of the herbicide effects on woody cover is apparent (Fig. 2A) and is consistent with results from Heaton et al. (2003) in which honey mesquite (*P. glandulosa*) cover did not fully recover to pre-herbicide levels 22 years after treatment. These findings point to the importance of accounting for past land uses, specifically brush management activities, in monitoring and forecasting potential changes in cover and biomass. In this regard, we present evidence through transition probabilities for *P. velutina* cover change which supports the idea that the maximum sustainable *P. velutina* cover at the SRER with mean annual precipitation of ca. 370-mm is ca. 30%. We propose that subsequent changes in land cover associated with woody plant encroachment will be expressed in stand structure rather than broad measures of abundance. Grazing did influence recovery from the herbicide with respect to stand structure with larger trees more evenly distributed, but not in total *P. velutina* biomass (Fig 5B, inset).

Ramifications for P. velutina biomass

The historical perspective on *P. velutina* biomass indicates that grazed and ungrazed landscapes can support further biomass increases in the future (circa 1948, Fig 5B); however, the means by which grazed and ungrazed stands reach maximum sustainable woody biomass will be different due to disparities in size structure. Partitioning *P. velutina* biomass into 20-m X 20-m subplots to compare mean and standard error estimates further illustrates the parametric interpretations that grazing effects on *P. velutina* biomass are indistinguishable in 2006 (182.3 ± 23.8 kg/400 m² on protected and 189.8 ± 47.7 kg/400 m² on grazed). Grazed and protected areas exhibited the same biomass; however, *P. velutina* constituents contrasted with fewer and larger trees on the grazed plot.

P. velutina biomass recovery from the 1965/66 herbicide treatment was not affected by livestock grazing, which falls in line with results from Noretto et al. (2006) that found no difference in above- or belowground carbon storage following 15 years of protection in northwest Patagonia. However, the disturbance history for the Patagonia site is not known, complicating direct comparisons. While 2006 total biomass is comparable on grazed and protected plots, *P. velutina* stands exhibit different stand structures and thus will likely have different potential carbon accumulation potentials.

Given distinct differences in *P. velutina* density and stand structure that coincide with similarities in overall biomass on grazed and protected plots, it is reasonable to assume that trajectories of change and future dynamics will manifest differently between plots. What might the future hold? Stands on both 2006 grazed and protected plots can

accommodate growth in medium and large size plants relative to past stand structure in 1948, yet reflect marked differences in *P. velutina* density. A potential outcome is that plants on the protected plot will experience self-thinning before those on the grazed plot. It is therefore likely that local associations for *P. velutina* density that reflect competitive interactions (i.e., high – low and low – high) will strengthen.

Spatial patterns of P. velutina density

Exploratory spatial pattern analysis presents opportunities to direct and design experimental and quantitative approaches to explore hypotheses (Fortin and Dale 2002). Our assessment revealed that removal of livestock significantly influenced spatial patterns in *P. velutina* density. Protection from livestock in 1932 hastened the development of hotspots for *P. velutina* recruitment (Fig. 7). Subsequent increases in *P. velutina* density have consequences for the distribution of soil nutrients with heightened inputs of carbon and nitrogen from woody plants, as well as for soil erosion, which follows decreases in herbaceous biomass. These findings represent an important first step toward elucidating mechanisms influencing *P. velutina* density and implications for ecosystem function (van de Koppel and Rietkerk 2004). We do not know the mechanism that yielded the spatial configurations, but our results provide a point from which to design future research to identifying pertinent ecological processes involved. With further research, outcomes could provide valuable insight to assessing consequences and benefits of livestock management practices in arid and semi-arid rangelands.

Models have been proposed to interpret spatial patterns of shrub distribution in an ecological context. First, Seifan and Kadmon (2006) suppose competitive effects of grasses deter successful woody seedling establishment. Their conceptual model predicts that livestock grazing will result in a more random distribution of shrub patches given decreased herbaceous cover that may displace recruits; our results support this outcome, however, without repeated measures of herbaceous ground cover in conjunction with observed changes, we are unable to link the observed pattern to the process generating it. Second, if woody cover has reached a dynamic equilibrium, we might envision spatial patterns in *P. velutina* distribution would reflect competitive interactions in the form of well distributed patterns in plant density. Although 5-m X 5-m cells did exhibit these associations, relationships were not strong. It could also be that the herbicide application that reset woody cover overwhelmed biotic processes that may have created stronger spatial patterns. We hypothesize that density dependent interactions will manifest and weaken the clustering pattern, yielding a more dispersed pattern in *P. velutina* density.

Conclusions

Historic land uses (e.g., livestock grazing, brush management) exert influence at a range of spatial scales (Peters and Havstad 2006). Widespread use of herbicides, especially in the 1950s and 1960s, and livestock grazing are common in actively managed landscapes of southwestern U.S.; both impose limitations for elucidating the role of biotic interactions in structuring population size distributions. For example, without knowing about the 1960s herbicide treatment, we could have easily concluded

that re-arrangement of cover and shifts in size class distributions were due to density-dependent regulation and self-organization. In efforts to effectively monitor rangeland health, we must acknowledge the strength and lasting legacy effects of historic events and processes on ecosystem function (Fredrickson et al. 2006). Demographic contributions to overall *P. velutina* biomass demonstrate the non-linear relationship between canopy size and aboveground biomass, highlighting the potential for error in estimating biomass with remote sensing. Remote sensing is reasonably considered the most effective means of monitoring surface characteristics across large areas (Wessman et al. 2004, Lu 2006); we advocate integration of field data and historic bottom-up perspectives to augment remote sensing approaches.

If, after decades of expansion, woody cover is reaching maximum potential in some regions (Browning et al. 2008), future changes will likely manifest in population size structure rather than overall plant cover. In this regard, spatial patterns and relationships will be important components of assessment to monitor stand structure (Kefi et al. 2007). The 74-year grazing contrast provides a rich field-based depiction of the influence of herbivory by cattle illustrating that in the absence of fire, grazing curtailed, rather than promoted *P. velutina* encroachment and precluded development of clustered patterns in *P. velutina* density. Although stand structure on protected plots was dominated by smaller plants, livestock grazing, in conjunction with an aerial herbicide, did not yield differences in total *P. velutina* biomass in 2006. This long-term field perspective affords important information regarding demographic contributions to woody

plant biomass, the potential for carbon uptake and storage, and long-term consequences of livestock management practices.

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Tables:

Table 1. Probability of increasing *P. velutina* cover within 20 m X 20 m subplots. Grazed and protected subplots ($n = 10$ each) were pooled across two time periods (1932 to 1948 and 1948 to 2006) to yield 40 transitions.

Initial <i>P. velutina</i> percent cover	Probability of increase
<= 10	1.0
11 – 20	0.8
21 – 25	0.8
26 – 30	0.5
> 30	0.0

Table 2. Global Moran's I values for *P. velutina* cover and density with 20-m X 20-m focal cells and their eight surrounding cells. P-values were derived from 999 random permutations.

	<u>Grazed</u>		<u>Protected</u>	
	Moran's I	p-value	Moran's I	p-value
Percent cover				
1932	-0.354	0.029	0.127	0.105
1948	-0.212	0.322	0.115	0.120
2006	-0.231	0.209	-0.181	0.363
Plant density				
1932	-0.133	0.546	-0.162	0.467
1948	-0.012	0.758	-0.136	0.547
2006	-0.182	0.382	-0.111	0.519

Figure Legends:

Fig. 1 Study area map illustrating the location of the McGinnies plots (C) on the Santa Rita Experimental Range (SRER) within the Sonoran Desert (A). The McGinnies plots occur at 1,100-m elevation on interfluves between adjacent drainages (B) depicted on a panchromatic 2005 image. Panel (C) illustrates the 200-m X 40-m subset of the North plot measured for this study (hatching). Stocking rates for cattle in the area are presented in panel (D) where dotted vertical lines denote the year *Prosopis velutina* measurements were taken.

Fig. 2 Mean (\pm Standard Error; n= ten 20-m X 20-m plots) velvet mesquite (*P. velutina*) canopy cover (%) (A) and plant density (B) on sandy clay loam soils at the Santa Rita Experimental Range. The study site was subject to year-round cattle grazing from 1912 to 1932, at which time exclosures were constructed. Density and cover values reported by Glendening (1952) for two 1.8-ha plots (88 – 20-m X 20-m subplots) were statistically comparable, pooled, and are represented with triangles. Results from repeated measures ANOVA are summarized in inset boxes. The area encompassing the plots was aerially treated with herbicides in May 1964 and 1965. Shrub cover measured within three 30-m X 30-m plots that were part of another study is presented as a control for herbicide treatment effects. Asterisks indicate significant differences for grazed and protected plots at $\alpha = 0.05$ with Tukey's test for differences in mean density and cover.

Fig. 3 Temporal dynamics of *P. velutina* canopy cover within a 200-m X 40-m area on the SRER on a sandy loam upland ecological site from 1932 to 2006. Red circles represent individual plant canopies in 1932 (red), 1948 (blue), 2006 (green). The entire

area was grazed by livestock from 1912 to 1932 at which time the right half the plot (0.4-ha, white region) was protected from livestock. The entire area was treated with aerial herbicides in May 1964 and 1965. Note general trend of canopy growth from 1932 to 1948 (A) (red within blue); and trend of canopy loss from 1948 to 2006 (B) (green within blue).

Fig. 4 Size class distribution of all *P. velutina* canopies within a 0.8-ha plot in 1932, 1948 and 2006. Half of the plot was protected from livestock starting in 1932 (white bars); cattle grazing was continued on the remaining area (gray bars). Inset tables include descriptive statistics; superscripts designate significant differences ($\alpha = 0.05$) in mean *P. velutina* canopy area.

Fig. 5 (A) Annual precipitation shown as the standardized difference (annual minus the long-term seasonal average divided by the standard deviation) for the Rodent Station rain gauge at 1,100-m elevation located 330-m from the study plots. A rain year corresponds to winter of a given year and the following summer (Oct to Sept). (B) Canopy size class contributions to total aboveground *P. velutina* biomass on two 0.4-ha plots (G = grazed by cattle since 1912 and P = protected from cattle since 1932). Inset box depicts mean (standard error) plant biomass in each plot (different subscripts denote differences at $\alpha = 0.05$). Biomass was derived from field measurements of plant canopy area in 1932, 1948, and 2006. Carbon mass was derived from biomass by applying a site specific conversion factor of 0.47 (Browning et al. 2008).

Fig. 6 Global Moran's I scatter plot for the number of *P. velutina* plants within 5 X 5-m subplots on grazed and protected plots in 1932 (A), 1948 (B), and 2006 (C). Moran's I (inset boxes) characterizes the relationship of a focal cell with its neighbors (in this case, eight cells). P-values based on 999 randomizations. Points in the upper right quadrant represent subplots of high plant density surrounded by high density neighbors (high:high); points in the lower right quadrant represent low density subplots surrounded by low density neighbors (low:low). To illustrate linkages between global and local measures of association, two subplots that deviated from mean density most strongly on the protected plot are circled in panels (B) and (C) and are denoted with hatching in Fig. 7.

Fig. 7 Local indicator of spatial association (LISA) cluster maps and associated Global Moran's I values for *P. velutina* plant density within 320 5-m X 5-m subplots (i.e., cells; dotted lines). Moran's I was calculated using 8-surrounding cells, a single spatial lag. The entire 200-m X 40-m area was grazed by livestock and lagomorphs until exclosures were established in 1932. Solid black outlines correspond to fence lines and symbols depict herbivores present. The top panel shows computations based on pre-treatment conditions for the "open range" when the study was initiated. The three bottom panels show patterns when Moran's I calculations corresponded to the various herbivore exclusion treatments. Mean (Standard Error) for *P. velutina* densities within 5-m X 5-m cells are reported below each panel. The lagomorph exclosure was not maintained after 1948. Cells exhibiting associations that deviate significantly from a random pattern are

represented with color and those cells exhibiting the strongest deviations from mean density are denoted in dark red. P-values are based upon 999 randomizations.

Fig. 1

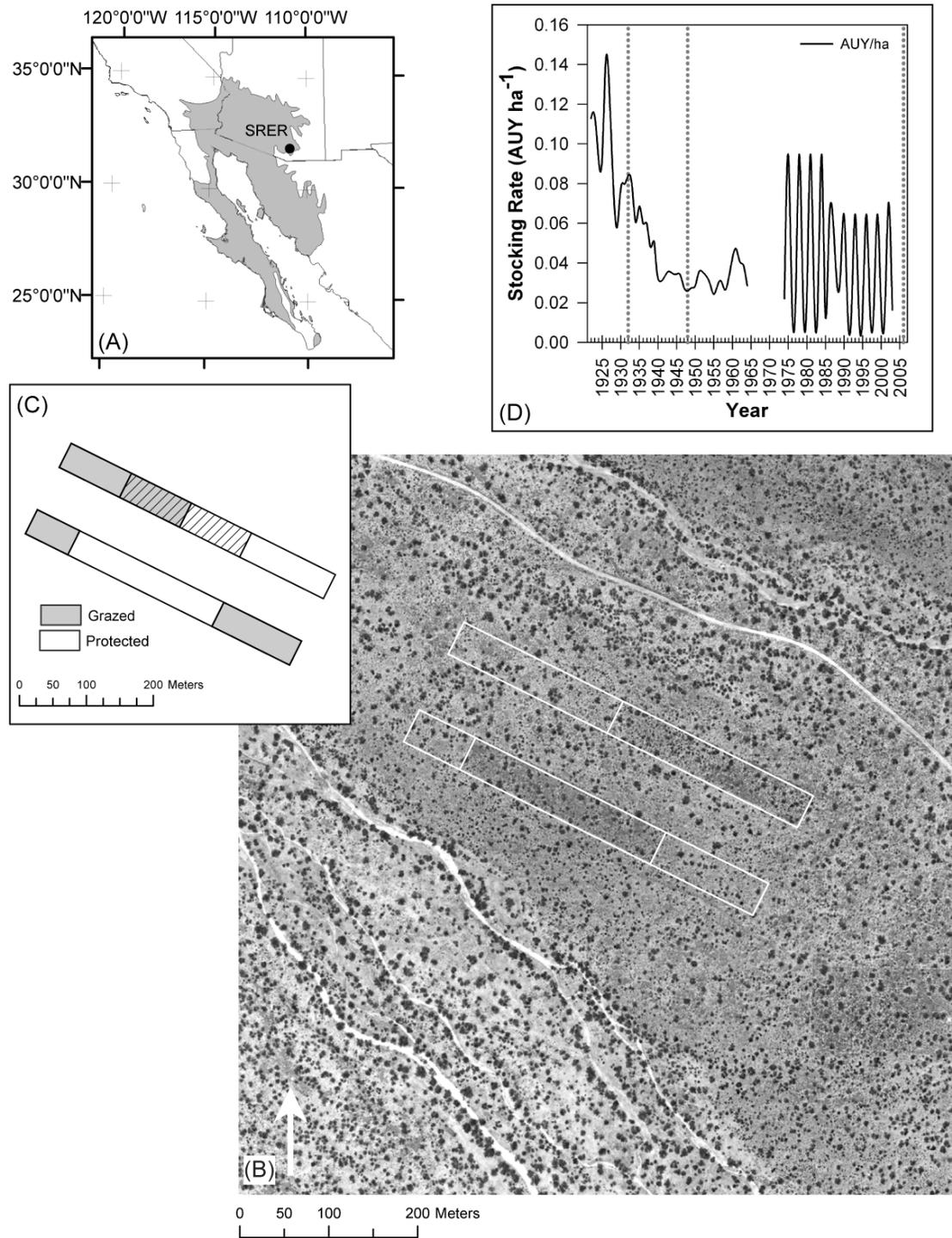


Fig. 2

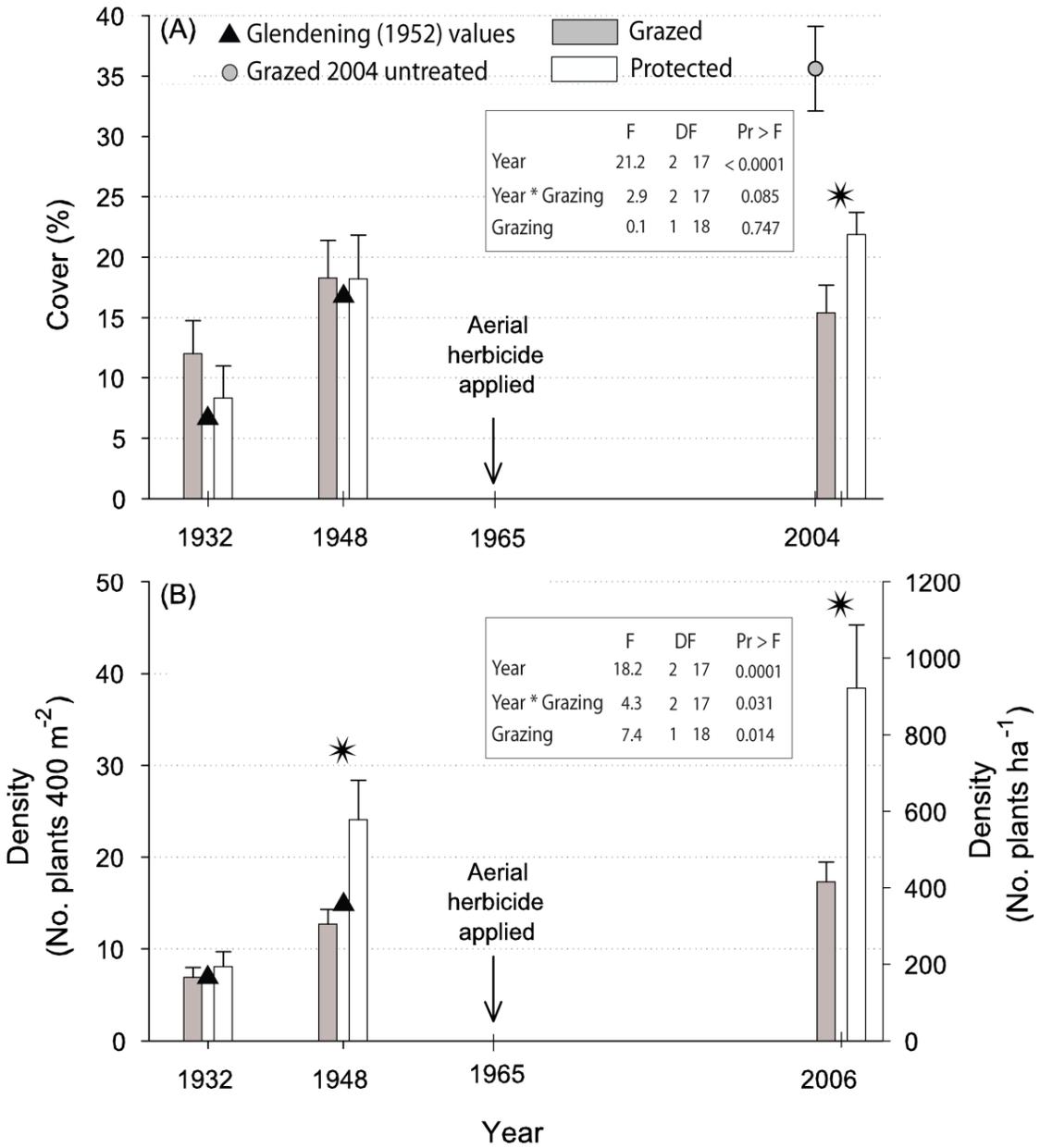


Fig. 3

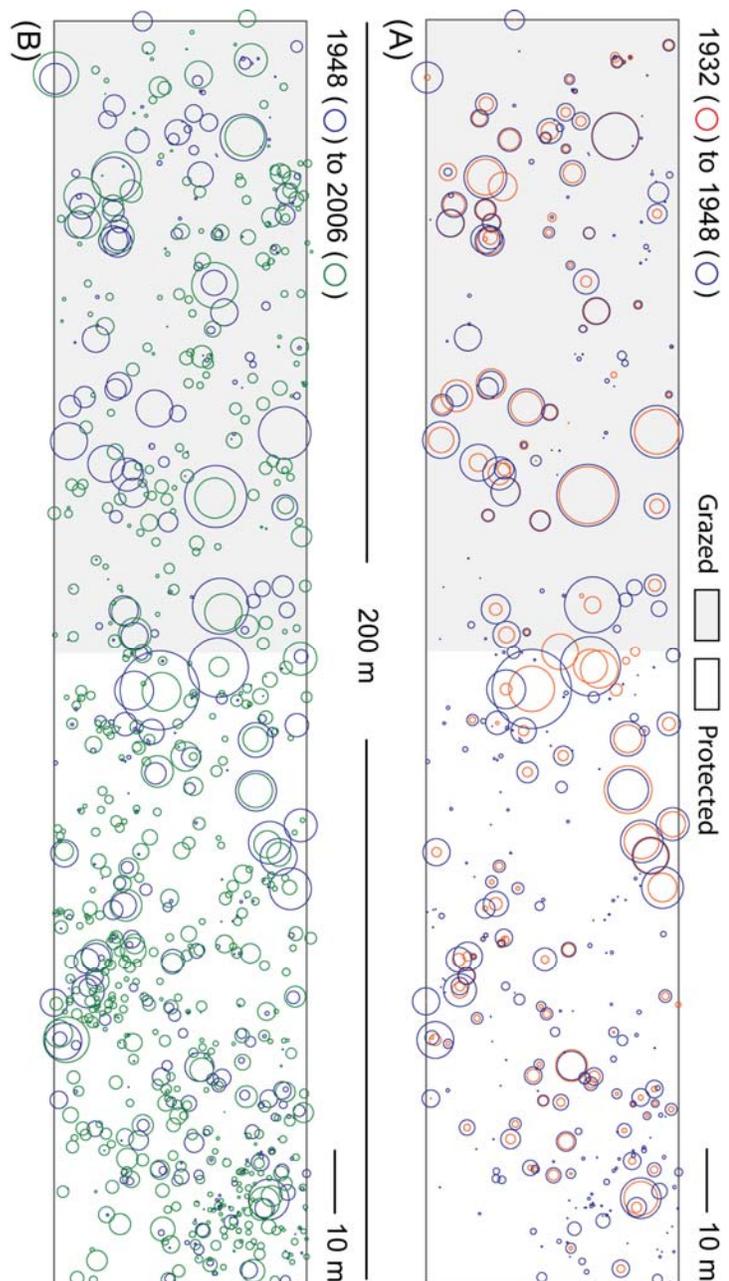


Fig. 4

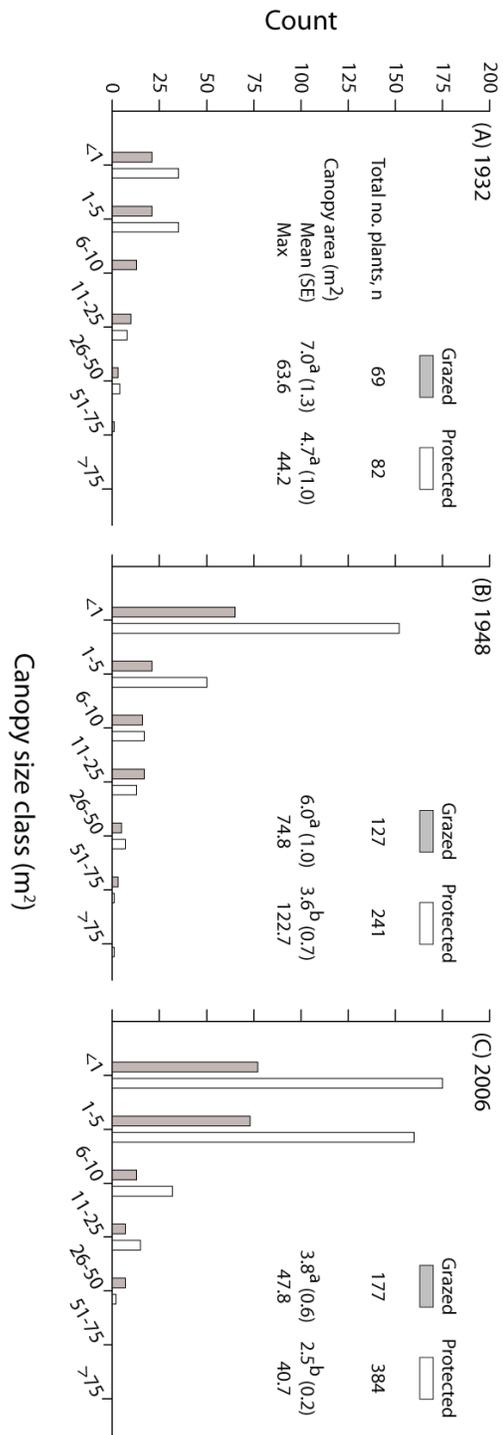


Fig. 5

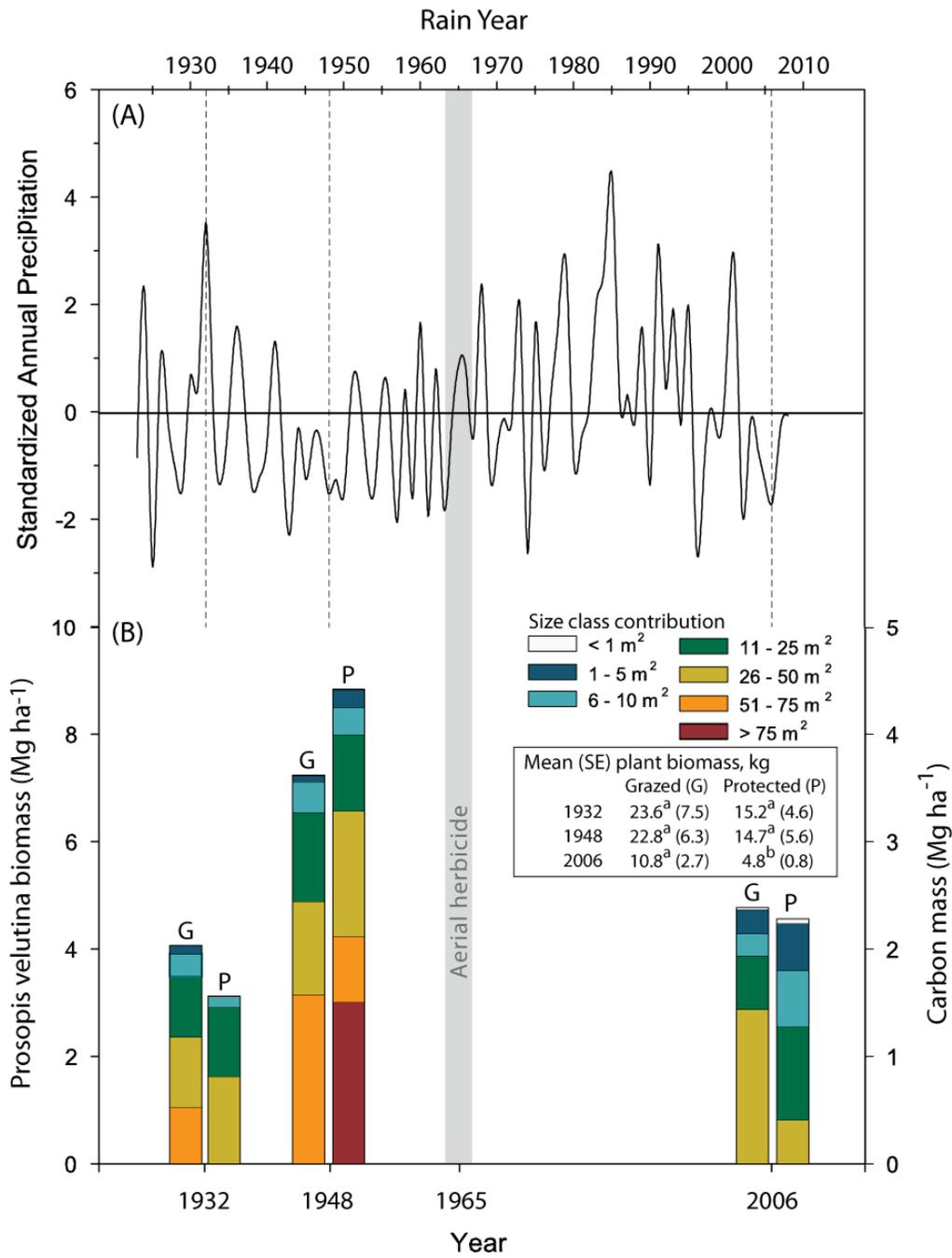


Fig. 6

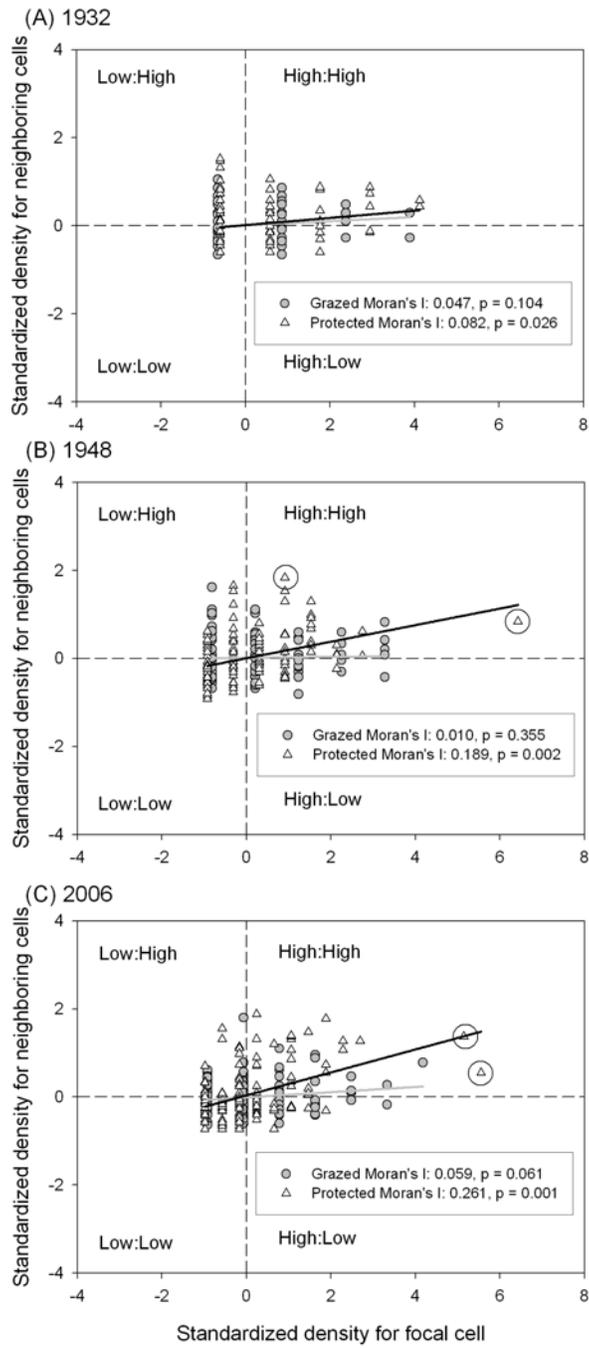


Fig. 7

