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A Quantitative Approach to the Development of Ecological Sites and State-and-Transition Models

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A QUANTITATIVE APPROACH TO THE DEVELOPMENT OF ECOLOGICAL SITES AND STATE-AND-TRANSITION MODELS

by

Matthew W. Van Scoyoc

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Eugene W. Schupp Major Professor	Barry B. Baker Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

A Quantitative Approach to the Development of Ecological Sites and State-and-Transition Models

by

Matthew W. Van Scoyoc, Master of Science

Utah State University, 2014

Major Professor: Dr. Eugene W. Schupp
Department: Wildland Resources

The interaction of land-use and climate can cause non-linear “state” changes in ecosystems, characterized by persistent differences in structure and function. Changes in land-use and climate on the Colorado Plateau may be driving many ecosystems toward undesired states where energy-intensive measures are required to return to previous states. Landscape classification systems based on “ecological potential” offer a robust framework to evaluate ecological conditions. Ecological sites are a popular landscape classification system based on long-term ecological potential and are widely used throughout the western US. Ecological sites have been described extensively for rangelands and woodlands on DOI Bureau of Land Management lands; however, they have yet to be described on USDA Forest Service (USFS) lands. In this thesis, I describe a statistical approach to ecological site delineation and the development of state-and-transition models, diagrams that illustrate ecosystem dynamics and responses to disturbances. In Chapter 2, I used a large inventory dataset and multivariate statistical procedures to classify plots based on life zone, soils, and potential vegetation, effectively delineating statistical ecological site-like groups. Most of the statistical ecological sites matched ecological sites already described by the USDA Natural Resources Conservation Service (NRCS). Additionally, I described one new ecological site that has not been described by the NRCS in the Colorado Plateau region. In Chapter 3, I examined empirical evidence for alternative states in mountain ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and upland piñon-juniper ecosystems. Using multivariate statistical procedures, I found that plots cluster into groups consistent with generalized alternative states identified in *a priori* conceptual models. Additionally, I showed that ponderosa pine clusters were true alternative states and piñon-juniper clusters were not true alternative states because they were confounded by similarities in climate. Ponderosa pine clusters were differentiated by overstory ponderosa pine density and corresponded to three states: *current potential*, *high fuel load*, and *reduced overstory*. These results illustrate the range of ecosystem variability that is present throughout the study area and present evidence for alternatives states caused by historical land-use. This project is the first to propose ecological sites and state-and-transition models on USFS lands in this region. These techniques could be applied to areas that do not have formally described ecological sites and state-and-transition models and could help identify ecological sites that may have been overlooked using other means of delineation. Additionally, these methods can be used to evaluate the range of ecological variability throughout an area of interest and to improved understanding of ecosystem dynamics.

(98 pages)

PUBLIC ABSTRACT

A Quantitative Approach to the Development of Ecological Sites and State-and-Transition Models

by

Matthew W. Van Scoyoc

Changes in land-use and climate can trigger changes in ecosystem conditions and may be driving ecosystems toward undesired “states” that provide inadequate ecosystem services. If these changes are drastic enough, energy intensive restoration programs are necessary to restore ecosystems to previous states. Landscape classification systems based on “ecological potential” offer a robust framework to evaluate and manage ecosystems. The ecological site concept is one such landscape classification system that has been developed by the USDA Natural Resources Conservation Service (NRCS) and describes ecosystems and ecosystem dynamics relative to “reference conditions” and response to disturbance. Ecological sites have gained popularity with land managers throughout the western U.S., and have been extensively described for DOI Bureau of Land Management agricultural lands and rangelands; however, they have yet to be described on USDA Forest Service (USFS) lands. In this thesis, I describe a statistical approach for developing ecological sites and state-and-transition models. In Chapter 2, I used a large dataset and multivariate statistics to classify plots based on life zone, soils, and potential vegetation, effectively describing statistical ecological site-like groups. Most of the statistical ecological sites matched ecological sites already described by the

NRCS. Additionally, I described one new ecological site that has not been described by the NRCS in the Colorado Plateau region. In Chapter 3, I examined evidence for alternative states in mountain ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and upland piñon-juniper ecosystems. Using multivariate statistics, I found that plots cluster into groups consistent with generalized alternative states described in *a priori* conceptual state-and-transition models. Additionally, I showed that ponderosa pine clusters were true alternative states and piñon-juniper clusters were not true alternative states because they were confounded by similarities in climate. These results illustrate the range of ecosystem variability that is present throughout the study area and present evidence for alternatives states caused by historical land-use. This project is the first to propose ecological sites and state-and-transition models on USFS lands in the region of our study area. These techniques could be applied to areas that do not have formally described ecological sites and state-and-transition models and could help identify ecological sites that may have been overlooked using other means of delineation. Additionally, these methods can be used to evaluate the range of ecological variability throughout an area of interest and to improved understanding of ecosystem dynamics.

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Matthew W. Van Scoyoc

PREFACE

This thesis is presented in journal format resulting in some redundancy among chapters. Chapter 2, “Statistical Methods for Landscape Classification Using the Principles of the Ecological Site Concept” is intended to be published in the journal Ecosphere. The format of this thesis follows that of Ecosphere with the necessary adaptations required by Utah State University, School of Graduate Studies.

For ease of presentation, scientific names of plant species are presented without authorities. All nomenclature follows A Utah Flora (Welsh et al. 2003) and plant codes follow USDA NRCS Plants Database (http://plants.usda.gov/).

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CHAPTER 1

INTRODUCTION

Landscape classification systems based on soil and vegetation characteristics that evaluate a range of ecological properties offer a robust approach to evaluating ecological conditions (Herrick et al. 2006). One such system is the ecological site classification system developed by the USDA Natural Resources Conservation Service (NRCS; Bestelmeyer and Brown 2010). Ecological sites have gained popularity with land managers and researchers, and provide a conceptual framework and communication tool for understanding ecosystem dynamics and responses to disturbances (Brown 2010). Differences between ecological sites are important because they affect the types of ecosystem services provided, create distinct expectations regarding land health and potential uses, and influence the success or failure of management actions (Bestelmeyer and Brown 2010). In this study, we utilize the ecological site concept to classify a large area of US Forest Service (USFS) land where no classification previously existed and explore alternative methods to determine ecological sites and states within these ecological sites.

Ecological sites

Ecological sites are recurrent features of the landscape with distinct soil, landform, geologic, and climatic characteristics, and potential plant communities that produce a variety of ecosystem services, or ecological potential, and respond similarly to land management actions, and natural and anthropogenic disturbances (Bestelmeyer et al. 2009, Moseley et al. 2010, NRCS 2013). They are a fine scale unit in the hierarchical landscape classification structure developed by the NRCS (Bestelmeyer and Brown 2010) and are correlated to NRCS soil survey geographic (SSURGO) soil components (Shiflet 1975, Duniway et al. 2010). The NRCS maps soils to soil map units that are composed of one to several soil components, each describing distinct soil types within the soil map unit. Similar soil components can support similar potential plant communities and have equivalent responses to management actions and disturbances (Duniway et al. 2010). The NRCS publishes ecological site descriptions (ESDs) summarizing the soil properties, climate, hydrology, landscape position, and plant community dynamics relative to disturbances and are interpreted relative to use and management of an ecological site (Bestelmeyer and Brown 2010, NRCS 2013).

The ecological site concept grew out of the range site concept that was historically used to evaluate the quantity and quality of vegetation on rangelands (Dyksterhuis 1949). The range site model used linear successional theory and indicator plants to evaluate production and assess trends in rangeland condition relative to acknowledged climax plant communities (Clements 1916, Sampson 1917, Dyksterhuis 1949). It became apparent that this model was unable to adequately predict future production and describe vegetation dynamics on rangelands when certain disturbances, such as establishment of invasive exotic plant species, derailed the modeled successional pathway (Westoby et al. 1989). This led to the adoption of the multiple stable state concept and non-equilibrium paradigm to describe ecosystem dynamics (Holling 1973, May 1977, Lauenroth et al. 1989, Laycock 1991). The acceptance of multiple stable states and non-equilibrium ecosystem dynamics also changed the emphasis from plant community composition to soil- and hydrology-based evaluation procedures of rangeland health (Pyke et al. 2002).

State-and-transition models

State-and-transition models (STMs) were developed to illustrate the multiple stable states of each ecological site (Fig. 1.1; Westoby et al. 1989, Bestelmeyer et al. 2003, Briske et al. 2005). Contemporary STMs illustrate 1) non-continuous and irreversible ecosystem dynamics between states, 2) the continuous and reversible dynamics within states, referred to as community phases and community pathways, 3) the mechanisms by which “transitions” between states occur, and 4) descriptions of the “thresholds” where changes in soil properties and the plant community prevent recovery to previous states (Bestelmeyer et al. 2004, Briske et al. 2008, Scheffer et al. 2009).

Early applications of STMs included the evaluation of the spatial variability of rangeland conditions by Ash et al. (1994), although the terminology and concepts were not formally defined. Over the years the vocabulary and concepts were debated and refined (Stringham et al. 2001, 2003, Bestelmeyer et al. 2003, 2009, 2010, Briske et al. 2005, 2006, 2008). It is now recognized that STMs should include both the non-continuous dynamics of multiple stable states and the continuous dynamics of climax community succession (Briske et al. 2005). In this thesis, we focus on states, community phases, transitions, and community pathways (Fig. 1.1).

States and transitions represent non-continuous and irreversible ecosystem dynamics that occur when “thresholds” are crossed. States are relatively permanent and usually require energy-intensive measures to return to previous states. The *reference state* symbolizes ecosystem dynamics before European settlement and defines the ecological potential of an ecological site (State 1 in Fig.1.1). The *current potential state* is similar to the *reference state* in function and structure but has undergone a state shift, such as the establishment of persistent exotic plant populations, and represents the most resilient state at present (State 2 in Fig. 1.1). Alternative states differ in their structure and function because the ecosystem has crossed a threshold that cannot be reversed through succession (State 3 in Fig.1.1). Transitions occur between states and represent mechanisms responsible for causing state shifts.

Community phases and pathways are nested within states (Fig. 1.1) and depict the continuous and reversible successional dynamics that are relatively temporary. Generally, there are reference phases that depict the structural and functional properties associated with the greatest resilience, and an “at-risk” phase that is more vulnerable to transitions to an alternative state. Community pathways illustrate mechanisms responsible for phase shifts and are usually the drivers of natural succession.

Research needs

The NRCS has published a vast array of ESDs for rangelands on federal, state, and private lands throughout the western U.S, and has recently started to describe ecological sites for woodlands and forests primarily on USDA Forest Service (USFS) lands (Townsend 2010). An iterative process is used to develop ecological site concepts, state-and-transition models, and ESDs consisting of 1) subjectively identifying ecological concepts and their importance to land management, 2) collecting data from these sites, and 3) analyzing data and testing concepts (Bestelmeyer et al. 2009, 2010, Moseley et al.

2010, NRCS 2013). Each round of development refines the ecological site and STM concepts as more data are collected at increasing levels of intensity. Low-intensity reconnaissance data are used to identify reference areas and acknowledged alternative states, while high intensity monitoring data are used to refine states, community phases, and other material presented in an ESD. In 2010, the NRCS, USFS, and Bureau of Land Management signed a memorandum of understanding to advance the use and development of ecological sites as a consistent method of classification to facilitate management across jurisdictional boundaries (NRCS 2013).

Although ecological sites and STMs have numerous advantages as a classification system and are becoming widely used, the process described above is fairly subjective and uses relatively low amounts of data to construct the models. In addition, the NRCS has many ecological sites where STMs have not been developed, and despite management needs for such models, there are not resources available to develop these models in a timely manner. To date, there has been little work done to identify ecological sites on USFS lands and few ESDs have been published for woodlands and forests (Townsend 2010). In Montana, the USFS has been working to “crosswalk” the USFS Terrestrial Ecological Unit Inventory system (Winthers et al. 2005) that classifies the landscape by ecological potential with ecological sites, but similar work has not been attempted on the Colorado Plateau.

More recent efforts have focused on alternative methods of identifying states within ecological sites when large inventory or monitoring databases are available, and much of this work has focused on ecosystems of the Colorado Plateau. Miller et al. (2011) used hierarchical clustering and principal components analysis on a large inventory data set to identify and describe alternative states of grasslands in southeast Utah. Bowker et al. (2013) used fuzzy clustering and non-metric multidimensional scaling ordinations on several large monitoring data sets, including two National Park Service Inventory and Monitoring data sets, to propose STMs for seven ecological sites on the Colorado Plateau. Utilizing large datasets to identify and describe alternative states incorporates more objectivity into the process of developing STMs. These alternatives to the methods used by the NRCS are important because 1) they are data driven methods of identifying alternative states and 2) they have the potential to identify new alternative states not conceptualized by the standard methods. Lastly, once states of ecological sites (i.e. boxes in Fig. 1.1) are defined, transitions (i.e. arrows in Fig. 1.1) need to be identified and tested.

In this study, we use hierarchical cluster analysis and non-metric multidimensional scaling ordinations on data from a large field-sampling effort to identify ecological sites and construct STMs in an area of the Colorado Plateau where they have yet to be developed. The Monticello Ranger District of the Manti-La Sal National Forest encompasses about 1300 km^2 of mountains, plateaus, and canyons on USFS lands in southeast Utah. Logging, livestock grazing, and climate have led to persistent changes in ecosystem properties, resulting in a range of putative alternative states throughout the study area. The goals of this study were to 1) propose ecological sites on USFS lands on the Colorado Plateau (Chapter 2) and 2) develop provisional state-and-transition models to gain a better understand of ecosystem dynamics in the study area (Chapter 3).

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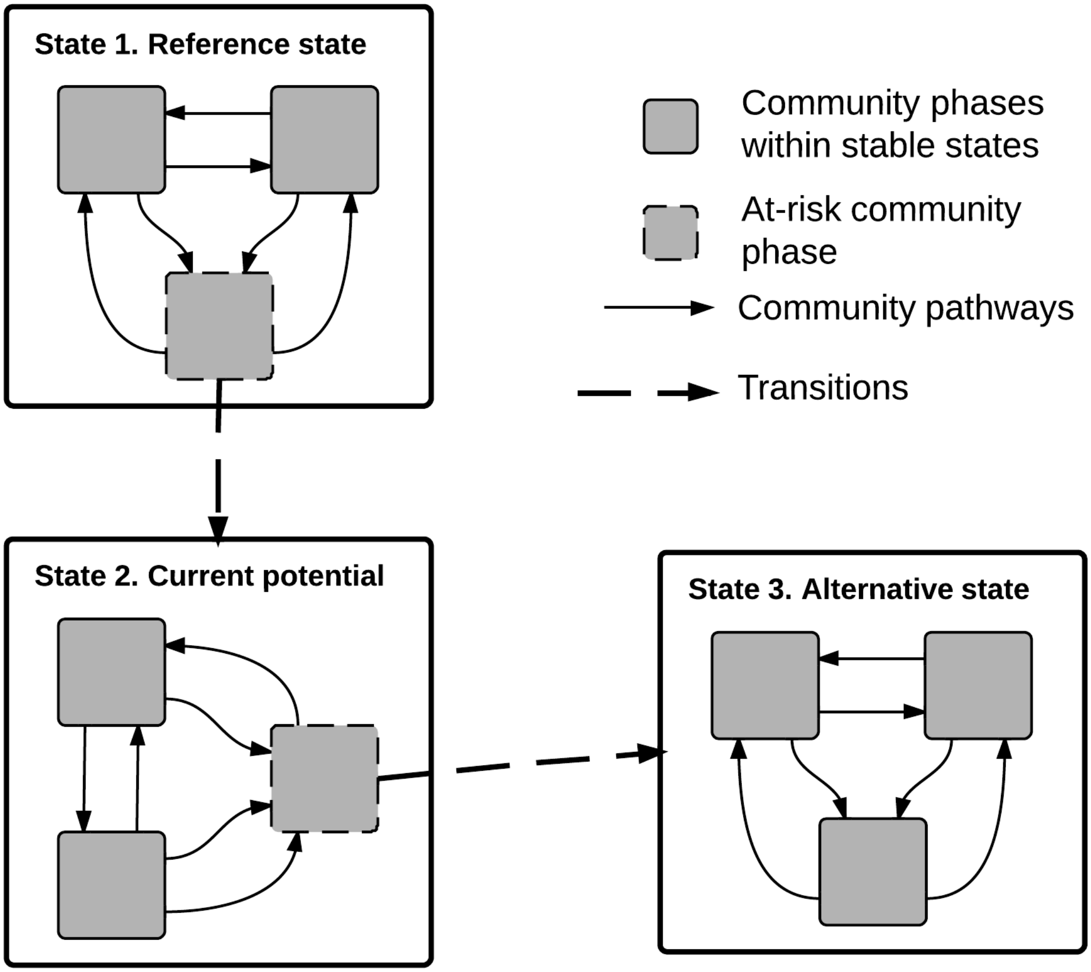

Fig. 1.1. Example state-and-transition model showing three stable states (large open boxes) and three community phases (small filled boxes) within each state. Transitions (dashed arrows) between states are discontinuous and irreversible without energy-intensive measures, while community pathways (solid arrows) among phases within states are reversible and continuous. The “at-risk” community phases (small filled box with dashed borders) are vulnerable to transitions to alternative states. Adapted from Briske et al. (2008).

CHAPTER 2

STATISTICAL METHODS FOR LANDSCAPE CLASSIFICATION USING THE PRINCIPLES OF THE ECOLOGICAL SITE CONCEPT[1]

Abstract

Ecological sites are a popular landscape classification system based on long-term ecological potential and are a widely used throughout the western US. Ecological sites have been described for a large portion of Bureau of Land Management and private agricultural and range lands, but have yet to be adequately described on other federal lands such as the US Forest Service (USFS). In this manuscript we describe a statistical approach to ecological site delineation using an inventory dataset collected on USFS lands where ecological sites have not been described and multivariate statistical procedures. We classified plots based on soils, life zone, and potential vegetation and effectively delineated statistical ecological site-like groups. Most of our statistical ecological sites matched ecological sites already described by the Natural Resources Conservation Service (NRCS) in other areas. Additionally we describe one new landscape-soil-vegetation association that has not been described by NRCS as an ecological site in our region. These methods can be used to evaluate the range of ecological variability throughout an area of interest and help identify ecological sites that may have been overlooked using other means of delineation.

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[1] This chapter is co-authored by Matthew W. Van Scoyoc, Jamin K. Johanson, and Eugene W. Schupp.

Introduction

Effectively managing landscapes for desirable ecosystem services requires knowledge of how ecosystems are changing through time, and management strategies need to be adaptable as the interactions between climate change and disturbances, both natural and anthropogenic, are anticipated to be complex (McKenzie and Allen 2007, Schwinning et al. 2008). Landscape classification systems based on soil and vegetation properties that produce a range of ecological services, or ecological potential, offer a robust way to evaluate ecological conditions (Herrick et al. 2006). There are a handful of landscape classification systems that land managers are currently using, including LANDFIRE (Rollins 2009) that was developed by the U.S. Department of the Interior and the USDA Forest Service (USFS), the USFS Terrestrial Ecological Unit Inventory system (TEUI; Winthers et al. 2005), and ecological sites (NRCS 2013) developed by the USDA Natural Resources Conservation Service (NRCS). The concept of ecological sites has gained in popularity with land managers and researchers and provides a conceptual framework for understanding ecosystem dynamics and responses to disturbances (Bestelmeyer and Brown 2010).

Ecological sites are distinct recurrent features of the landscape with similar soil, landform, geologic, and climatic characteristics, and with similar potential plant communities that have comparable responses to land management actions and natural disturbance (Herrick et al. 2006, NRCS 2013). They are not specific locations within a landscape; instead, they are units of a classification system that describe a range of ecological properties and processes. Ecological sites are a fine scale unit in the hierarchical land resource classification structure developed by the NRCS that includes major land resource areas (MLRAs), land resource units, and soil map units (Bestelmeyer and Brown 2010). MLRAs are based on climatic, physiographic, plant geographic and land-use differences and are similar to Bailey's Ecoregions and The Nature Conservancy Ecoregions. Land resource units subdivide MLRAs by regional climate and/or geomorphology and are again divided into complexes of characteristic soils called soil map units. Ecological sites reclassify soil map units by vegetation and ecological processes (Duniway et al. 2010).

The predecessor of the ecological sites concept, range sites, were described for rangelands using indicator plant communities to classify and interpret ecological potential and the biological resources a site can produce in terms of rangeland management (i.e. forage; Dyksterhuis 1949, Shiflet 1975). This type of classification system relies on a portion of the landscape that is free of disturbance (Brown 2010) and is of little use to land managers, especially where there has been extensive natural or anthropogenic disturbance (Herrick et al. 2006). We now understand that differences in ecological sites are primarily due to differences in soil properties (e.g., soil texture and depth) within a climatic zone (Tugel et al. 2005, Bestelmeyer et al. 2006, Duniway et al. 2010) and the plant communities are the expressed response to disturbance history.

The effective application of the ecological site concept requires a document known as an ecological site description (ESD). ESDs describe the range of variability, including reference plant communities, and the patterns and mechanism that lead to alternative ecological states (Bestelmeyer et al. 2004, 2010). Contained with ESDs arestate-and-transition models that contrast the properties of the reference and alternative states, describe the mechanisms by which transitions among states occur, and describe the thresholds at which changes in the soil and plant community prevents recovery without energy-intensive measures to return to previous states (Bestelmeyer et al. 2004, Scheffer et al. 2009).

Ecological sites have been described for a large portion of Bureau of Land Management and private agricultural and range lands, but have yet to be adequately described for forests and woodlands on other federal lands such as the US Forest Service, although Jeb Williams and others (unpublished) have been working to “crosswalk” TEUI classifications and ESDs in Montana. The current methods for developing ecological sites begin with subjectively identifying ecological concepts that are relevant to land managers and then collecting and analyzing data from an area of interest to test the concepts (Bestelmeyer et al. 2009, 2010, Moseley et al. 2010, NRCS 2013). This approach uses relatively little data to construct ecological concepts and might be overlooking landscape-soil-vegetation relationships that are important for land managers and researchers to consider.

Our study follows the premise of the ecological site concept and uses quantitative techniques to classify the landscape based on ecological potential. Previous studies have used hierarchical clustering methods to examine ecological states within described ecological sites (Miller et al. 2011, Bowker et al. 2013). This study uses similar multivariate statistical techniques to classify sampling plots using current vegetation and inherent soil properties (i.e. soil depth and texture). Our primary goals were to 1) use multivariate statistical procedures to classify plots in a comparable way to ecological sites and 2) to compare the statistical classification to the ecological site assignment using expert knowledge.

Methods

Study area

Our study area was in the Monticello Ranger District of the Manti-La Sal National Forest in southeastern Utah, in MLRA 48A, the southern Rocky Mountains. The ranger district encompasses about 1300 km^2 of mountains, plateaus, and canyons, ranging in elevation from 1710-3463 m. For the plots sampled, winter mean precipitation ranges from 108-350 mm and summer mean precipitation ranges from 104-218 mm; winter mean temperatures range from 2.9˚-1.2˚C and summer mean temperature ranges from 13.9˚-22.1˚C (1981-2010 PRISM data, Daly et al. 2008). Dominant vegetation types include piñon-juniper woodlands at lower elevations, ponderosa pine forests at middle elevation, and mixed conifer forests at upper elevations, with sagebrush shrublands and grasslands dispersed throughout the study area. Contemporary land-use includes cattle grazing and recreation. Historically, livestock grazing and logging have been major land-use activities throughout the ranger district (USFS, *personal communication*).

Sampling design

One hundred and forty-eight plots were sampled throughout the study area from late May to late August in 2011 and 2012 (Fig. 2.1). Sampling points were selected using a stratified spatially balanced random sampling design in ArcGIS 9.3 (ESRI 2009). Slopes too steep to safely and efficiently sample (>40%) were removed from the sampling frame using a landscape accessibility model developed by the National Park Service (Garman 2005). To provide inference from sampling points to ecosystems, the sampling frame was based on soil map units from an order-three soil survey (USFS, *unpublished*), similar to an NRCS soil survey geographic (SSURGO) database. Soil map units that were dominated by rock outcrops were removed from the sampling frame to increase sampling efficiency. The Reversed Randomized Quadrant Recursive Raster method was used to generate 300 spatially balanced random sampling points (Theobald et al. 2007). Because we were interested in the grassland ecosystems and they make up 0.5% of the land cover throughout the study area, we targeted 30 extra points predicted to be grasslands from the southwest Regional Gap Analysis Project data (Lowry et al. 2007). Each point was the center of a potential 1-ha macro-plot. Most plots consisted of three 50-m transects spaced 25 m apart and oriented perpendicular to the slope, and were intended to sample the center of 1-ha. Where initial transects crossed vegetation, soil, or geomorphic boundaries, plot centers were adjusted up to 35 m to ensure that sampling was restricted to a single ecological site. If the plot layout could not be adjusted to accommodate a relatively homogeneous ecosystem, the sampling point was rejected. For efficiency, plots located in dense oak/mixed montane shrubs consisted of a 1600-m^2 macro-plot with 20-m transects spaced 10 m apart.

Field and lab measurements

Field sampling measurements were selected to quantify the structural and functional attributes related to ecosystem variability and were based on rangeland monitoring protocols (Herrick et al. 2009) and National Park Service (2003) forest and woodland fire monitoring procedures. Many measurements were taken on the plots, but only plot photos, vegetation cover, tree density, surface soil texture, and soil profiles including pedon depth and rock fraction were used in these analyses. Plot photos were taken at the plot center in the four cardinal directions and down transects at the start and end of each transect. Understory vegetation cover (vegetation <2 m in height) was calculated from line-point intercept at 1 m intervals along each transect (Herrick et al. 2009). Overstory tree density was calculated from a census of trees larger than 15 cm diameter at breast height (DBH) in the upper left quadrant of the plot (National Park Service 2003). Soil pits were dug ≈10 m downslope from the plot center to measure pedon depth and rock fraction and to describe soil profiles (Schoeneberger et al. 2002). To quantify surface soil texture, composite samples of the top 10-cm of soil were collected at five predetermined random locations along each transect. In the lab, soil surface texture was calculated using the hydrometer method (Gee and Bauder 1979).

Statistical classification

Nested Wards hierarchical cluster analyses and non-metric multidimensional scaling (NMDS) were conducted to classify plots into groups with similar ecological potential (Fig. 2.2). Wards hierarchical cluster analysis minimizes within group variance (Borcard et al. 2011) and was used to classify plots by vegetation type and then by soil type for each vegetation type separately. The effectiveness of the cluster analysis can be summarized by two statistics: 1) the agglomerative coefficient (AC), which measures the structure of the cluster analysis, with values closer to 1 specifying more structure, and 2) the cophenetic correlation coefficient (CC), which measures the accuracy of cluster analysis, with values near 1 indicating higher accuracy (Legendre and Legendre 2012). NMDS is an unconstrained ordination technique that represents the ordered relationships among objects in reduced ordination space and was used to illustrate and describe clusters (Borcard et al. 2011). NMDS was iterated 100 times or until a stable solution was reached. The stress function measures how far the ranked order is from being monotonic to the original distance matrix and is synonymous to variance. Stress values less than 0.2 indicate a good solution (McCune et al. 2002).

The primary cluster analysis was conducted using perennial understory vegetation cover and overstory tree density to group plots by vegetation type. Plots described as grasslands (n=11) in the field were removed from the data frame prior to analysis to allow more precise, accurate, and interpretable clusters. Hellinger transformation has been shown to be effective with community data (Legendre and Gallagher 2001) and was used to calculate dissimilarity between plots. In addition to NMDS, indicator species analyses (De Cáceres and Legendre 2009) were used to describe vegetation type clusters. Specificity (A statistic), the probability a site belongs to the target group given a species is present, and overall significance (p-value) were the primary statistics used from multi-level species pattern analysis and species combinations, although sensitivity (B statistic), the probability of finding the species in the target group, was taken into consideration.

Secondary cluster-NMDS analyses were then conducted using soil pedon depth, pedon rock fraction, and surface soil texture for each vegetation type separately to classify soil types within vegetation type clusters and to assess ecological potential of each cluster. The grassland plots that were removed for the vegetation type cluster analysis were included in this and all following analytical steps. This time, Euclidean distance was used to calculate dissimilarity because we were no longer using community data. Plots in alternative states of vegetation types that were potentially classified in the wrong cluster were identified using two diagnostic statistics, the NMDS goodness of fit statistic and silhouette widths from the cluster analysis.

The NMDS goodness of fit statistic was used to identify plots with soil properties that had poor ordinal fit with the rest of the cluster. The NMDS goodness of fit statistic is calculated so that sum of squared values for each plot is equal to squared stress and large values indicate poor ordinal fit (Oksanen et al. 2013). Examination of all NMDS goodness of fit statistics for all observations for each vegetation type concluded that goodness of fit statistics greater than 0.03 indicating a plot’s soil properties had poor ordinal fit for the given vegetation community.

Silhouette widths were used to identify plots where the soil type was misclassified. Silhouette widths are the average dissimilarity between an observation and all the other observations within its cluster compared to the dissimilarity of that observation and its neighboring cluster (Rousseeuw 1987). Observations with silhouette widths near one are accurately classified, those near zero lie between two clusters, and observations that are negative are misclassified. Examination of silhouette widths for all observations of each vegetation type concluded that soil properties were potentially misclassified for silhouette widths less than 0.2.

All analyses were conducted in R 3.0.2 (R Core Team 2013) using cluster 1.14.4 (Maechler et al. 2013), pvclust 1.2-2 (Suzuki and Shimodaira 2011), labdsv 1.6-1 (Roberts 2012), vegan 2.0-9 (Oksanen et al. 2013), and indicspecies 1.7.0 (De Cáceres and Legendre 2009) packages.

Assessing ecological potential

To validate the accuracy of the diagnostic statistics to identify potential alternative states, plot photos, soil profiles, and plant community data were assessed for each plot identified by the diagnostic statistics (by MWVS). These were compared to plot photos, soil profiles, and plant community data of plots that were representative of the potential vegetation community to determine if they fit better as an alternative state of that vegetation community than the one they were classified in by the vegetation type cluster analysis. Plots with a vegetation type that were clearly in an alternative state were reassigned to the appropriate potential vegetation type.

Additionally, all plots were assessed to identify plots in alternative states that were missed by the diagnostic statistics. Plot photos, soil profiles, and plant community data were examined, and plots potentially in alternative states were compared to those plots that were representative of the potential vegetation community. Plots with a vegetation type that were clearly in an alternative state were reassigned to the appropriate potential vegetation type. Plots within vegetation types with small sample sizes were reclassified to more specific vegetation types at this time.

Assembling statistical ecological sites

Lastly, a final soil type cluster analysis was conducted to classify and describe the soils for each vegetation type separately using soil pedon depth, rock fraction, and surface texture. Elevation and vegetation type were used to classify the following life zones: upland, mountain, high mountain, and subalpine (Lowry et al. 2007, section 7). A naming system modeled after what the NRCS uses for ecological sites (NRCS 2006, NRCS 2013) was then implemented using life zones, slope, soil types, and vegetation types.

Classification using expert knowledge

Climate data, plot photos, soil profiles, elevation, slope, aspect, and vegetation data were used to assign the most appropriate existing ecological site name and number to each plot using expert knowledge (by JKJ) and NRCS databases. Average annual precipitation was calculated for each plot using 30-year (1971-2000) climatology from the Parameter-elevation Relationships on Independent Slopes Model (PRISM) dataset (Daly et al. 2008) in ArcGIS 10.1 (ESRI 2013) and resampled at 100-m gird-size using the cubic convolution option. The climate summaries in conjunction with elevation, slope, and aspect were used to estimate the soil moisture regime for each plot. The Utah Ecological Site Index (https://esis.sc.egov.usda.gov/Welcome/pgESDWelcome.aspx) was then used as a framework for ecological site designations.

Results

Vegetation type cluster analysis

Primary vegetation type cluster analysis was highly structured (AC=0.98) and accurate (CC=0.74), yielding seven vegetation type clusters (Fig. 2.3): aspen forests (n=11), mixed conifer forests (n=5), oak/mixed montane shrubs (n=16), piñon-juniper woodlands (n=39), piñon pine woodlands (n=10), ponderosa pine forests (n=40), and sagebrush shrublands (n=16). The first two NMDS axes explained 85.5% of the variance of the data (stress=0.145), and was the best solution after 100 iterations. When environmental and soil variables were fitted to the NMDS, the first axis was correlated with elevation, soil texture, pedon depth, and geographic position (i.e., on the east side of the study area) and the second axis with aspect, elevation, pedon depth, and soil texture.

Indicator species analysis was used to describe vegetation type clusters (see Tables A1 and A2 in Appendix). Aspen forests were dominated by overstory *Populus tremuloides*, and understory *P. tremuloides, Achnatherum nelsonii*, *Osmorhiza depauperata*, *Calamagrostis canadensis*, and *Arnica cordifolia* cover. In mixed conifer forests, *Abies concolor* and *Pseudotsuga menziesii* were significant components of both the overstory and understory plant composition. Oak/mixed montane shrubs were characterized by *Quercus gambelii*, *Amelanchier* spp., *Symphoricarpos* spp., and *Poa pratensis*. *Juniperus osteosperma* and *Pinus edulis* were prevalent in both the overstory and understory of piñon-juniper woodlands. Piñon pine woodlands were dominated by *P. edulis*, *Pedicularis centrathera*, and *Poa fendleriana*. In ponderosa pine forests, *P. ponderosa* was the most abundant overstory tree species and a major component of understory cover. Lastly, sagebrush shrublands were characterized by a combination of *Artemisia tridentata*, *Purshia tridentata*, and *Gutierrezia sarothrae*.

Soil type cluster analysis

Soil type cluster analysis was conducted on seven vegetation types; plots identified as grasslands (n=11) were included in this and all following analyses, but mixed conifer forest was excluded due to the small sample size of this vegetation type (n=5).

The diagnostic statistics identified 39 of the 143 plots used in the soil type cluster analysis (26%) as potential alternative states of other vegetation types (Table 2.1). Details of plots identified and reclassified within each vegetation type are included below.

Aspen forests. Two clusters were differentiated for aspen plots: loams and stony loams (Fig. 2.4A). Within the aspen vegetation type, two plots were identified as potential alternative states of other vegetation types by the diagnostic statistics (Table 2.1). However, neither plot was determined to be an alternative state of another vegetation type and was not reclassified.

Grasslands. Two clusters were differentiated for grassland plots: stony loams and loams (Fig. 2.4B). Within the grassland vegetation type, two plots were identified as potential alternative states of other vegetation types by the diagnostic statistics (Table 2.1). One plot was reclassified as oak/mixed montane shrubs (Table 2.1).

Oak/mixed montane shrubs. Two clusters were differentiated for oak/mixed montane shrub plots: sandy loams and stony loams (Fig. 2.4C). Within the oak/mixed montane shrub vegetation type, seven plots were identified as potential alternative states of other vegetation types by the diagnostic statistics (Table 2.1). Two were reclassified; one as ponderosa pine and the other as sagebrush (Table 2.1).

Piñon pine woodlands. Two clusters were differentiated for piñon pine plots: loams and stony sandy loams (Fig. 2.4D). Within the piñon pine woodlands, two plots were identified as potential alternative states of other vegetation types by the diagnostic statistics; neither was reclassified (Table 2.1).

Ponderosa pine forests. Three clusters were differentiated for ponderosa pine plots: loams, stony loams, and stony sandy loams (Fig. 2.4E). Within ponderosa pine forests, six plots were identified as potential alternative states of other vegetation types by the diagnostic statistics, and none were reclassified (Table 2.1).

Piñon-juniper woodlands. Three clusters were differentiated for piñon-juniper plots: loams, sandy loams, and stony sandy loams (Fig. 2.4F). Within piñon-juniper woodlands, 17 plots were identified as potential alternative states of other vegetation types by the diagnostic statistics (Table 2.1). Two were reclassified as oak/mixed montane shrubs, two were reclassified as ponderosa pine forests, three were reclassified as sagebrush, and ten plots were not reclassified (Table 2.1).

Sagebrush shrublands. Three clusters were differentiated for sagebrush plots: loams, sandy loams, and stony loams (Fig. 2.4G). Within sagebrush shrublands, three plots were identified as potential alternative states of other vegetation types by the diagnostic statistics (Table 2.1). One was reclassified as oak/mixed montane shrubs (Table 2.1).

Assessing ecological potential

The diagnostic statistics identified 39 of the 143 plots used in the soil type cluster analysis (26%) as potential alternative states of other vegetation types (Table 2.1). Eleven of the 39 plots (28%) were determined to be correctly identified as potential alternative states of other vegetation types using plot photos, soil profiles, and plant community data for each plot and were reassigned to more appropriate vegetation types (by MWVS).

When assessing plots that were missed by the diagnostic statistics, an additional 33 plots (22% of the 148 plots) were identified as alternative states of vegetation types other than the type classified by cluster analysis, and these plots were reassigned to more appropriate vegetation types using plot photos, soil profiles, and plant community data. Plots were also reclassified in two vegetation types with small sample sizes. The mixed conifer forest vegetation type was separated into Douglas fir forest (n=3) and spruce-fir forest (n=2) plots. In addition, one bigtooth maple plot was separated from the oak/mixed montane shrub vegetation type.

Comparison of ecological site designations

The statistical classification successfully delineated most of the sampling plots by ecological site. The combination of life zones, soil types, and potential vegetation communities yielded 40 statistical ecological sites that follow the premise of the established ecological site concept (Table 2.2). Twenty of our statistical ecological sites have been conceptualized by the NRCS (including published and unpublished ESDs). Nineteen of the 40 statistical ecological sites could reasonably be renamed to match existing ecological sites in neighboring MLRAs due to redundancies in the naming scheme. For example, the classification of “sandy loam” in the statistical ecological site Upland Sandy Loam (Piñon Pine) can be shortened to “loam” because the NRCS includes sandy loams in the soil description section of Upland Loam (Piñon Pine) ESDs. One statistical ecological site, Mountain Sandy Loam (Ponderosa Pine), is not named or described for MLRA 48 in Utah; distinguishing this new site type is likely very relevant to land managers (Table 2.2).

The statistical ecological site classification matched the ecological site assigned by expert knowledge (by JKJ, see Methods) for 41 of the 148 plots (27.7%), and another 60 statistical ecological sites (41.5%) matched existing ecological sites in neighboring

MLRAs. Using the rationale mentioned in the Upland Sandy Loam (Piñon Pine) example above, 36 plots (24.3%) could reasonably be renamed to match existing ecological sites in MLRA 48 or neighboring MLRAs. Using these methods, 137 of 148 (92.6%) statistical ecological sites matched previously described ecological sites.

Discussion

Using current vegetation and examining the soil properties within vegetation types, we were able to classify plots by ecological site and propose ecological sites in an area that does not have published ESDs. Most of the statistical ecological sites matched ecological sites that have been described by the NRCS, and one new ecological site was proposed for MLRA 48. The assembly of these statistical ecological sites not only helps to validate the ecological site concept by using data to construct ecological site concepts, but proposes new techniques for identifying potential ecological sites that may be of concern to land managers.

This statistical procedure has also identified one soil-vegetation-landscape association that has not been described by the NRCS in MLRA 48, which should be important to land managers, Mountain Sandy Loam (Ponderosa Pine). This new ecological site describes a unique combination of soil and landform properties that influences the vegetation community, and may have different responses to disturbance and restoration activities than described in previous ecological sites for the region. The current ecological site used for ponderosa pine ecosystems in MLRA 48 is Mountain Loam (Ponderosa Pine), although the NRCS has conceptualized and/or described Mountain Cobbly Sandy Loam and Shallow Sandy Loam (Ponderosa Pine) sites in other

MLRAs in Utah. The Mountain Sandy Loam (Ponderosa Pine) distinction has significant implications for land managers in terms of the water holding capacity of the soil that can affect plant productivity and other management actions. Sandy loams have lower available water capacity than do loams (Gupta and Larson 1979, Saxton and Rawls 2006), which can decrease forest productivity (Gholz et al. 1990, Sampson and Allen 1999) and may have important implications for management strategies such as silviculture, grazing plans, and restoration projects.

A limitation of this statistical method is that alternative states that are far removed from the *reference* or *current potential state* due to disturbance or management history are misclassified and difficult to identify. The success of the diagnostic statistics to identify potential alternative states was fairly ineffective; 39 plots (out of 143) were identified by the diagnostic statistics, and 11 (of 39) were reclassified to more appropriate vegetation types. Evaluating each site individually using plot photos, soil pedon descriptions, and vegetation data was more effective at identifying alternative states.

Implications for land management

Due to the socio-geographic location of our study area, there are no reference communities available to use as indicators for baseline conditions. Thus, we evaluated the *current potential* through statistical means, and our best guess at reference communities comes from the literature and published ESDs. All of the accessible lands that one can get to by foot or vehicle throughout the study area have evidence of human activities, mostly logging and livestock grazing. The ponderosa pine forests on the ranger district were logged in the 1960’s and 1970’s and are mostly second growth (USFS, *personal* *communication)*. Unrestricted livestock grazing in the late 1800’s and early 1900’s, lead to degradation in many areas throughout the study area. Although present-day USFS grazing plans have reduced the grazing impacts through fencing grazing allotments, developing water sources, and implementing pasture rotations, overgrazing still occurs in some areas (USFS, *personal communication)*.

The Abajo Mountains and Elk Ridge that compose the Monticello Ranger District are an isolated island mountain range. They share similarities with mountain ranges like the San Juan Mountains (MLRA 48) to the east, the Wasatch Range (MLRA 47) to the northwest, and the small mountain ranges throughout northern Arizona and New Mexico (MLRA 39) to the south. Our statistical methods are the first attempt to describe and evaluate ecological potential in this area.

The construction of ecological sites has been largely a qualitative exercise (Moseley et al. 2010). Bestelmeyer et al. (2009) describe an eight step method for the development of ecological sites that begins with synthesizing ecological concepts and testing the concepts with smaller data sets before collecting high intensity inventory data. The methods presented here start with high intensity inventory data and use quantitative techniques to identify potential ecological sites. Refinements of ecological site concepts are the next steps in this process, including local knowledge (Knapp and Fernandez-Gimenez 2009) followed by low to medium intensity sampling to verify concepts. Lastly, implementation of long-term monitoring plots can be established using the existing high intensity plots and additional sampling locations can easily be added if necessary or desired (Theobald et al. 2007).

The primary goal of this study was to classify plots in a manner similar to ecological sites, while removing subjectivity from the process. By creating an iterative procedure that classifies current vegetation communities and examines the associated soil properties, we were able to evaluate the ecological potential of ecosystems in our study area. This process has allowed us to create a classification scheme comparable to the ecological site concept. This method could be useful in areas that have no published ESDs when land managers or researchers need to evaluate areas or study plots based on ecological potential, such as USFS lands.

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Table 2.1. Potential alternative states of other vegetation types that were identified by diagnostic statistics and the reclassified vegetation type. Bold face type indicate the diagnostic metric that identified the plot as an outlier. If the reclassified column is blank, the plot was not reclassified.

Plot	**NRCS ecological site designation**	**NMDS Goodness of fit statistic**	**Cluster analysis silhouette width**	**Reclassified**
Aspen				
M108	High Mountain Loam (Aspen)	0.01	**0.04**	
M137	High Mountain Loam (Aspen)	0.01	**0.12**	
Grasslands				
MG014	High Mountain Loam (Browse)	0.03	**-0.31**	Oak/Mixed Montane Shrubs
MG024	High Mountain Windswept Ridge (Fringed sagebrush)	0.02	**-0.16**	
Oak/Mixed Montane Shrubs				
M029	Mountain Shallow Loam (Oak)	**0.04**	**0.18**	
M034	Mountain Loam (Oak)	**0.03**	0.46	
M037	Mountain Shallow Loam (Ponderosa Pine)	0.02	**0.12**	Ponderosa Pine
M083	Mountain Shallow Loam (Oak)	0.02	**0.04**	
M095	Mountain Loam (Oak)/Mountain Loam (Mountain Big Sagebrush)	**0.05**	**-0.19**	
M105	Mountain Shallow Loam (Oak)	**0.04**	**-0.11**	
M106	Mountain Loam (Oak)/Mountain Loam (Mountain Big Sagebrush)	0.03	**-0.01**	Sagebrush
Piñon Pine				
M081	Upland Stony Loam (Piñon – Utah Juniper)	0.01	**0.19**	
M185	Mountain Loam (Oak)/Mountain Loam (Mountain Big Sagebrush)	0.01	**0.12**	
Piñon-Juniper				
M001	Upland Shallow Loam (Two-Needle Piñon / Utah Juniper)	0.02	**0.16**	
M035	Upland Shallow Loam (Two-Needle Piñon / Utah Juniper)	**0.03**	**-0.01**	
M040	Mountain Shallow Loam (Oak)	0.02	**-0.09**	
M051	Upland Loam (PJ)	0.02	**0.08**	
M052	Upland Loam (PJ)	**0.03**	**0.13**	
M054	Mountain Shallow Loam (Oak)	0.02	**-0.02**	Oak/Mixed Montane Shrubs
Piñon-Juniper continued				
M057	Upland Stony Loam (Piñon-Utah Juniper)	**0.03**	0.30	
M084	Upland Stony Loam (PJ)	0.02	**0.03**	

Plot	NRCS ecological site designation	NMDS Goodness of fit statistic	Cluster analysis silhouette width	Reclassified
M057	Upland Stony Loam (Piñon-Utah Juniper)	0.03	**0.30**	
M103	Upland Shallow Loam (Two-Needle Piñon / Utah Juniper)	**0.03**	0.23	
M107	Mountain Shallow Loam (Ponderosa Pine)	0.02	**0.17**	Ponderosa Pine
M111	Upland Shallow Loam (Bonneville big sagebrush)	0.02	**0.13**	Sagebrush
M123	Mountain Loam (Oak)	0.02	**-0.06**	Oak/Mixed Montane Shrubs
M140	Mountain Loam (Ponderosa Pine)	**0.03**	0.33	Ponderosa Pine
M152	Mountain Shallow Loam (Mountain Big Sagebrush)	**0.04**	0.24	Sagebrush
M154	Upland Stony Loam (Piñon-Utah Juniper)	0.01	**-0.10**	
M171	Upland Stony Loam (Piñon-Utah Juniper)	0.02	**0.17**	
M173	Mountain Shallow Loam (Mountain Big Sagebrush)	0.01	**0.10**	Sagebrush
Ponderosa Pine				
M025	Mountain Loam (Ponderosa Pine)	0.01	**-0.08**	
M027	Mountain Loam (Ponderosa Pine)	0.01	**0.15**	
M044	Mountain Loam (Ponderosa Pine)	0.01	**0.17**	
M046	Mountain Loam (Ponderosa Pine)	0.01	**0.16**	
M082	Mountain Shallow Loam (Ponderosa Pine)	0.01	**0.11**	
M180	Mountain Shallow Loam (Ponderosa Pine)	0.01	**0.00**	
Sagebrush				
M031	Mountain Loam (Oak)/Mountain Loam (Mountain Big Sagebrush)	0.01	**-0.10**	
M086	Upland Shallow Loam (Bonneville big sagebrush)	**0.03**	0.22	
M128	Mountain Shallow Loam (Oak)	0.01	**-0.05**	Oak/Mixed Montane Shrubs

Table 2.2. Statistical ecological site names and the number of plots sampled. Including whether the statistical name matched an existing NRCS ecological site name, whether the statistical name was redundant, and whether the statistical ecological site is new.

Statistical ecological site name	**Number of plots sampled**	**Status**	**NRCS Ecological Site Name**
High Mountain Loam (Aspen)	2	Matched NRCS	High Mountain Loam (Aspen)
High Mountain Stony Loam (Meadow)	2	Matched NRCS	High Mountain Stony Loam (Meadow)
High Mountain Stony Loam (Oak/Mixed Montane Shrubs)	2	Matched NRCS	High Mountain Stony Loam (Browse)
High Mountain Stony Loam (Sagebrush)	2	Matched NRCS	High Mountain Stony Loam (Big Sagebrush)
Mountain loam (Meadow)	2	Matched NRCS	Mountain loam (Meadow)
Mountain loam (Oak/Mixed Montane Shrubs)	2	Matched NRCS	Mountain loam (Browse)
Mountain Loam (Aspen)	5	Matched NRCS	Mountain Loam (Aspen)
Mountain Loam (Douglas Fir)	2	Matched NRCS	Mountain Loam (Douglas Fir)
Mountain Loam (Ponderosa Pine)	34	Matched NRCS	Mountain Loam (Ponderosa Pine)
Mountain Loam (Sagebrush)	1	Matched NRCS	Mountain Loam (Big Sagebrush)
Mountain Steep Loam (Ponderosa Pine)	3	Matched NRCS	Mountain Steep Loam (Ponderosa Pine)
Mountain Stony loam (Aspen)	2	Matched NRCS	Mountain Stony loam (Aspen)
Mountain Stony Loam (Meadow)	2	Matched NRCS	Mountain Stony Loam (Meadow)
Mountain Stony Loam (Sagebrush)	3	Matched NRCS	Mountain Stony Loam (Big Sagebrush)
Upland loam (Oak/Mixed Montane Shrubs)	12	Matched NRCS	Upland loam (Browse)
Upland loam (Piñon-Juniper)	7	Matched NRCS	Upland loam (Two-needle Piñon Pine-Utah Juniper)
Upland Loam (Piñon Pine)	2	Matched NRCS	Upland Loam (Two-needle Piñon Pine)
Upland Loam (Sagebrush)	6	Matched NRCS	Upland Loam (Big Sagebrush)
Upland Sandy loam (Sagebrush)	7	Matched NRCS	Upland Sandy loam (Big Sagebrush)
Upland Sandy Loam (Piñon-Juniper)	10	Matched NRCS	Upland Sandy Loam (Two-needle Piñon Pine-Utah Juniper)
Upland Stony Loam (Oak/Mixed Montane Shrubs)	3	Matched NRCS	Upland Stony Loam (Browse)

Statistical ecological site name	**Number of plots sampled**	**Status**	**NRCS Ecological Site Name**
Upland Stony Loam (Piñon-Juniper)	5	Matched NRCS	Upland Stony Loam (Two-needle Piñon Pine-Utah Juniper)
Upland Stony Loam (Sagebrush)	2	Matched NRCS	Upland Stony Loam (Big Sagebrush)
High Mountain Very Stony Loam (Oak/Mixed Montane Shrubs)	1	Redundant name	High Mountain Stony Loam (Browse)
Mountain Silty Clay Loam (Bigtooth Maple)	1	Redundant name	Mountain Loam (Bigtooth Maple)
Mountain Steep Sandy Clay Loam (Mixed Conifer)	1	Redundant name	Mountain Steep Loam (Mixed Conifer)
Mountain Very Stony Loam (Aspen)	1	Redundant name	Mountain Stony Loam (Aspen)
Mountain Very Stony Loam (Oak/Mixed Montane Shrubs)	1	Redundant name	Mountain Stony Loam (Browse)
Subalpine Steep Loam (Spruce-Fir)	1	Redundant name	Subalpine Loam (Spruce-Fir)
Subalpine Steep Stony Loam (Meadow)	1	Redundant name	Subalpine Stony Loam (Meadow)
Subalpine Steep Very Stony Loam (Oak/Mixed Montane Shrubs)	2	Redundant name	Subalpine Stony Loam (Browse)
Subalpine Very Steep Stony Loam (Meadow)	1	Redundant name	Subalpine Stony Loam (Meadow)
Upland Sandy Loam (Piñon Pine)	3	Redundant name	Upland Loam (Two-needle Piñon Pine)
Upland Steep Stony Loam (Oak/Mixed Montane Shrubs)	1	Redundant name	Upland Loam (Browse)
Upland Steep Stony Loam (Piñon-Juniper)	1	Redundant name	Upland Steep Loam (Two-needle Piñon Pine-Utah Juniper)
Upland Very Steep Sandy Loam (Piñon-Juniper)	1	Redundant name	Upland Steep Loam (Two-needle Piñon Pine-Utah Juniper)
Upland Very Steep Stony Loam (Oak/Mixed Montane Shrubs)	1	Redundant name	Upland Loam (Browse)
Upland Very Stony Loam (Oak/Mixed Montane Shrubs)	2	Redundant name	Upland Loam (Browse)
Mountain Sandy loam (Ponderosa Pine)	11	New Ecological Site	NA

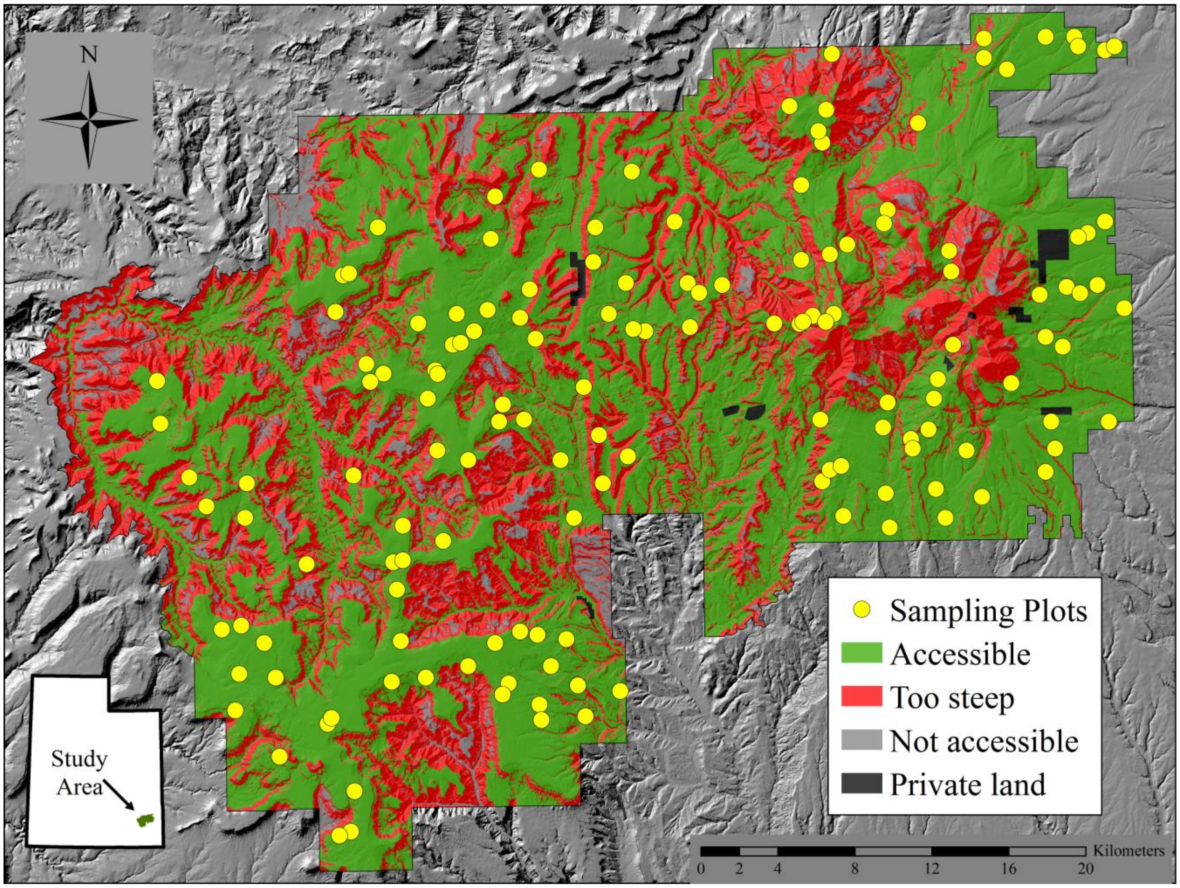

Fig. 2.1. The distribution of sampling points throughout the Monticello USFS Ranger District in southern Utah. Sampling points (yellow circles) are located on accessible areas (green). Areas that are too steep (red) or not accessible (grey), and private lands (black) have been removed from the sampling frame using an NPS accessibility model (Garman 2005).

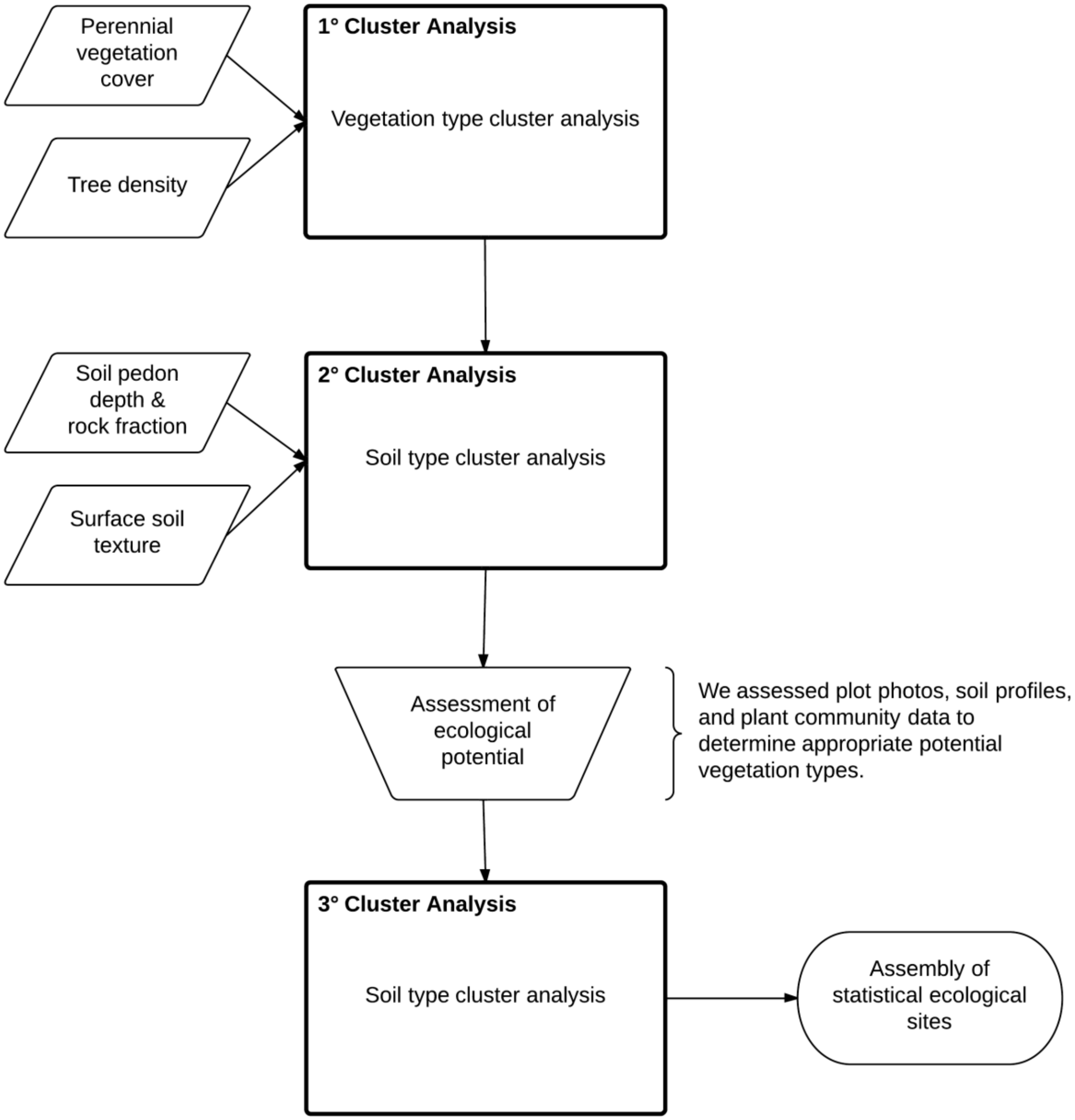

Fig. 2.2. Flow chart showing statistical procedure for classification of ecological sites. Slanted squares represent data sets, bold rectangles represent statistical procedures, the trapezoid represents manual input, and the oval represents the final product.

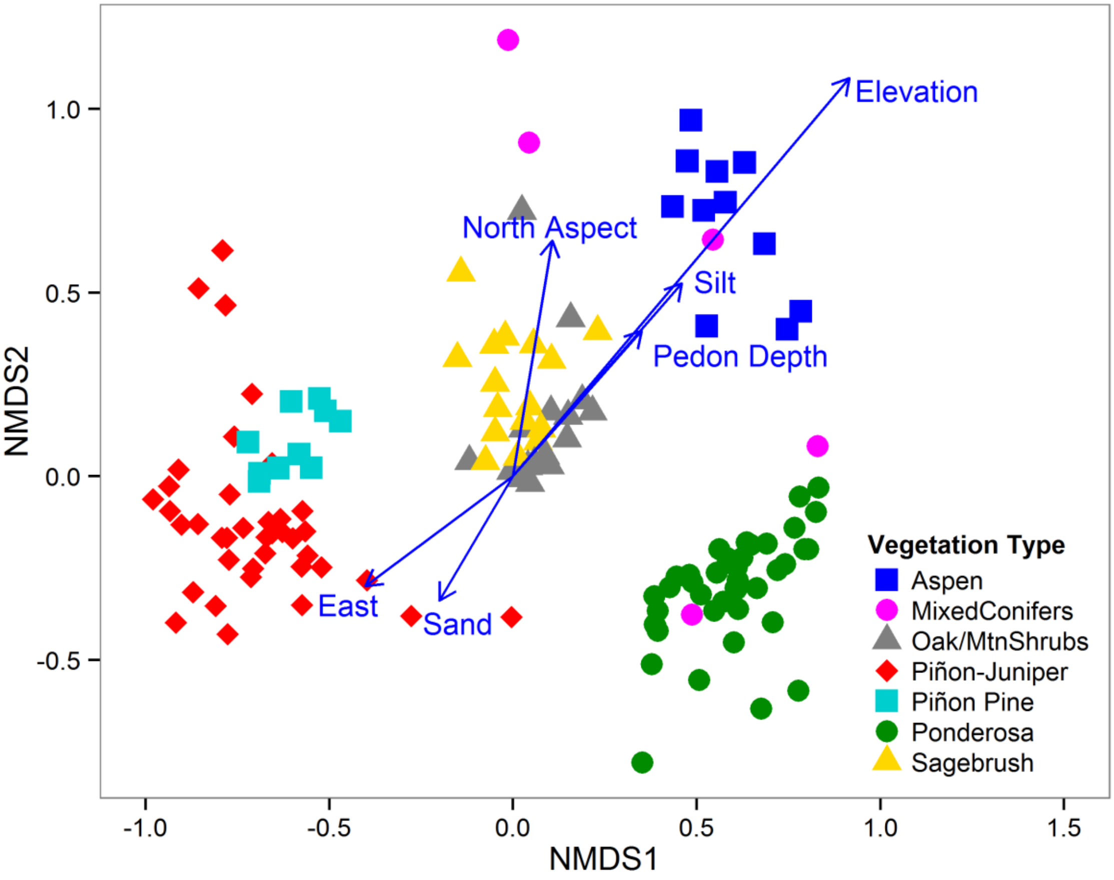

Fig. 2.3. NMDS biplot illustrating clusters from vegetation type cluster analysis. Vectors indicate significant environmental and soil properties contributing to the clusters and length of vector indicates relative significance. The first two axes explained 85.5% of the variance of the data (stress=0.145).

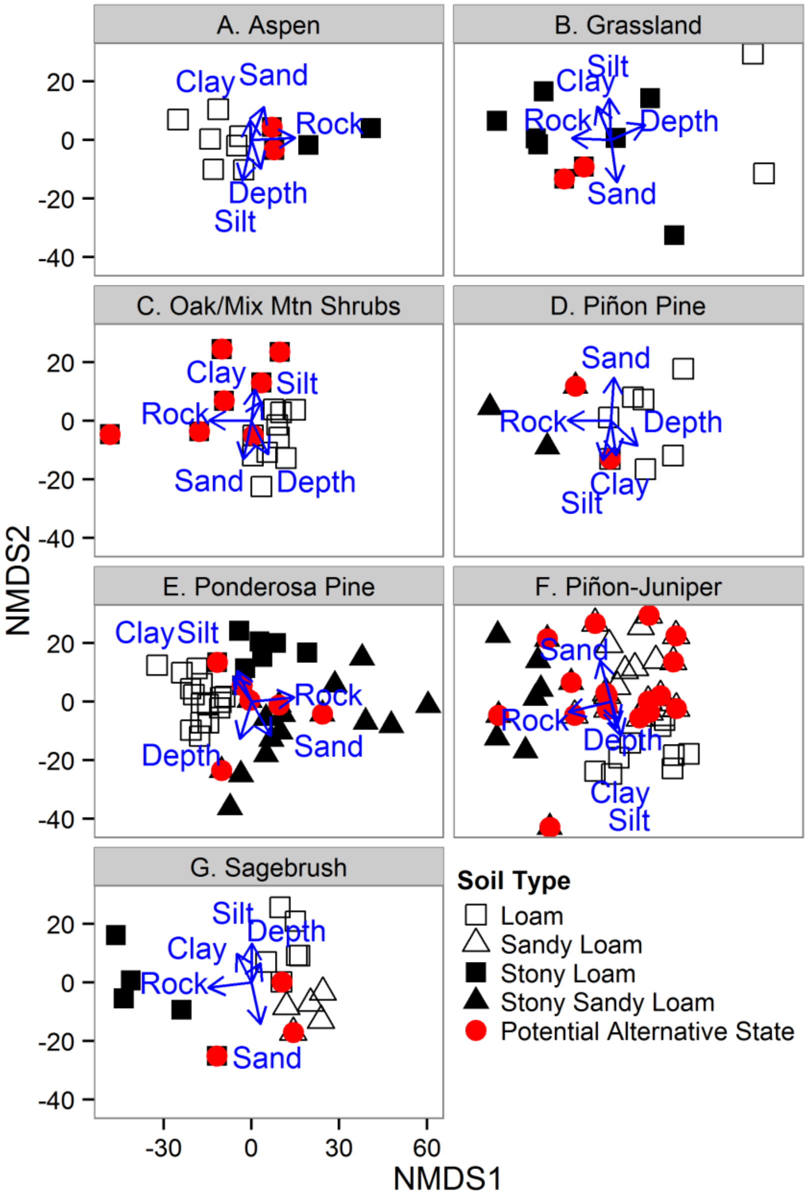

Fig. 2.4. NMDS biplots of soil properties for each vegetation type highlighting potential alternative states of other vegetation types(red) identified by the NMDS goodness of fit statistic and/or silhouette widths (see Table 2.1). Vectors illustrate the influence of soil properties on the ordination, and length of vector represents relative significance. A) Two clusters were differentiated for aspen plots: loams and stony loams. Two plots were identified as potential alternative states of other vegetation types were identified. B) Two clusters were differentiated for grassland plots: stony loams and loams. Two plots were

identified as potential alternative states of other vegetation types. C) Two clusters were differentiated for oak/mixed montane shrub plots: sandy loams and stony loams. Seven plots were identified as potential alternative states of other vegetation types. D) Two clusters were differentiated for piñon pine plots: loams and stony sandy loams. Two were identified as potential alternative states of other vegetation types. E) Three clusters for differentiated for ponderosa pine plots: loams, stony loams, and stony sandy loams. Six plots were identified as potential alternative states of other vegetation types. F) Three clusters for differentiated for piñon-juniper plots: loams, sandy loams, and stony sandy loams. Seventeen plots were identified as potential alternative states of other vegetation types. G) Three clusters for differentiated for sagebrush plots: loams, sandy loams, and stony loams. Three plots were identified as potential alternative states of other vegetation types.

CHAPTER 3

A MULTIVARIATE APPROACH TO IDENTIFYING ALTERNATIVE STATES

Abstract

Persistent differences in ecosystem structure and function distinguish alternative states of ecosystems. We examined empirical evidence for alternative states in mountain ponderosa pine (*Pinus ponderosa*) and upland piñon-juniper ecosystems on U.S. Forest Service lands in southeast Utah, where topographic complexity from canyons and mountains has led to spatial variation in logging and livestock grazing. Using hierarchical cluster analysis and nonmetric multidimensional scaling, we found that plots cluster into groups consistent with generalized alternative states identified in *a priori* conceptual models. Using canonical correspondence analysis, we show that ponderosa pine clusters were likely true alternative states but that piñon-juniper clusters were confounded by climate. Ponderosa pine ecosystem clusters were differentiated by overstory ponderosa pine density and corresponded to three states: *current potential*, *high fuel load*, and *reduced overstory*. Piñon-juniper ecosystem clusters were differentiated by overstory Utah juniper (*Juniperus osteosperma*) and piñon pine (*Pinus edulis*) densities and plant and bare ground cover that corresponded to two states: *current potential* and *eroded*. Our results illustrate the range of ecosystem variability that is present throughout the study area. These techniques could be applied to areas that do not have formally-described state-and-transition models, such as US Forest Service lands, to improve understanding of ecosystem dynamics and help land managers evaluate management strategies.

Introduction

Persistent differences in ecosystem structure and function distinguish alternative states of ecosystems. Ecological states are plant communities and associated dynamic soil properties (i.e. depth or texture) that create distinct, persistent structural and functional ecosystem characteristics (Stringham et al. 2003, Bestelmeyer et al. 2009). State shifts, or transitions, are caused by mechanisms, like climate or land-use, that trigger relatively major changes in soil properties, plant community structure, and/or disturbance regimes that limit recovery to the former state (Chapin et al. 1996, Folke et al. 2004, Bestelmeyer et al. 2010). For land managers, alternative states are of concern because 1) they differ in their capacity to provide ecosystem services and support management objectives (Suding and Hobbs 2009, Miller et al. 2011) and 2) climate and land-use may cause non-linear transitions to undesired states (Scheffer and Carpenter 2003, Briske et al. 2006).

State-and-transition models (STMs) are diagrams that illustrate ecosystem dynamics and include narratives that describe how changes in alternative states occur (Bestelmeyer et al. 2010). STMs are valuable tools that provide insight for management and restoration targets, degradation risk assessment, and monitoring programs for adaptive management strategies (Bestelmeyer et al. 2004, 2010, Knapp and Fernandez-Gimenez 2009). From a management perspective, it is useful to identify states that maintain ecosystem resilience (Briske et al. 2008). States with higher resiliency offer a wide range of ecosystem services and are able to recover more quickly after disturbance events.

STMs depict multiple acknowledged or hypothesized stable states that can occupy an ecological site and illustrate non-continuous and irreversible ecosystem dynamics between states, and continuous and reversible dynamics within states (Briske et al. 2005). They also describe the mechanisms by which state shifts, or transitions, occur and describe the “thresholds” at which changes in the dynamic soil properties and plant community prevents recovery to previous states (Bestelmeyer et al. 2004, Scheffer et al. 2009; Fig. 1.1). The *reference state* symbolizes ecosystem dynamics before European settlement and describes the ecological potential of a site. The *current potential state* functions similarly to the *reference state* but has undergone a state shift, usually the establishment of persistent exotic plant populations, and represents the most resilient state at present. *Alternative states* differ in their structure and function because the ecosystem has crossed a threshold that cannot be reversed in a timely manner through natural succession. Transitions occur between states and represent mechanisms responsible for causing state shifts. Community phases and pathways are nested in states and depict continuous and reversible successional ecosystem dynamics that are relatively temporary (Fig. 1.1). Generally there is a reference phase that depicts the structural and functional properties with the greatest resilience, and an “at-risk” phase that is vulnerable to transitions to state shifts. Community pathways illustrate mechanisms responsible for phase shifts and are usually the drivers of successional ecosystem dynamics.

In this study we examine evidence of the existence of alternative states in two prominent ecosystems on USDA Forest Service (USFS) lands on the Colorado Plateau in southeast Utah where STMs have not been developed, mountain ponderosa pine forests and upland piñon-juniper woodlands. These ecosystems differ in management and disturbance regimes, and constructing STMs for these systems will provide a flexible framework for adaptive management strategies.

Ponderosa pine forests on the Colorado Plateau are susceptible to state changes due to prolonged fire suppression that has altered the natural fire cycle (Allen et al. 2002). Examples of alternative states in ponderosa pine forests follow two common patterns. The first state is characterized by a persistent increase of small diameter ponderosa pine densities and understory shrubs and reinforced by decreased fire frequency that results in stressed mature trees and high fuel loads (Allen et al. 2002). The second state is characterized by a dramatic reduction of the overstory canopy and replacement of the shrub and perennial grass dominated understory community by oak (*Quercus gambelii*) and greenleaf manzanita (*Arctostaphylos patula*), often as the result of bark beetle mortality or stand-replacing fire (Noss et al. 2006).

Piñon-juniper woodlands can shift to alternative states in response to the interactions of drought and land-use (Betancourt et al. 1993, Miller and Wigand 1994, Barger et al. 2009). Examples of alternative states in piñon-juniper woodlands follow three common patterns. The first state is characterized by persistent populations of exotic plants in the understory, resulting in nutrient cycling feedbacks that reinforce the altered plant community (Bashkin et al. 2003). The second state is characterized by dominant invasive annuals in the understory accompanied by increased fire frequency and severity that cause tree mortality resulting in an annualized state (Miller and Tausch 2000). The third state is caused by repeated or heavy surface disturbances that facilitate soil degradation, persistent declines in the understory vegetation community, and increased canopy cover (Miller and Wigand 1994, Davenport et al. 1998).

Other studies have used multivariate statistics to identify and describe alternative states in grasslands (Miller et al. 2011, Bowker et al. 2013). Bestelmeyer et al. (2009)

proposed that if the occurrence of different states does not relate to differences in soil or climatic properties, then they are true alternative states that reflect spatial variation in historical events. In this study, we use similar methods to classify and describe plots from a large inventory data set using resilience-based STMs. More specifically, we examined evidence for alternative states in mountain ponderosa pine forests and upland piñon-juniper woodlands on USFS lands where there are no published STMs for these vegetation communities. To examine the validity of the proposed STMs, we examined the relationships between ecosystem structure and climate, and ecosystem structure and soil properties.

Methods

Study area

The Monticello Ranger District of the Manti-La Sal National Forest, in southeast Utah, ranges from 1710 m to 3463 m in elevation and encompasses about 1300 km^2 of mountains, plateaus, and canyons on the Colorado Plateau. Ponderosa pine communities cover about 24,096 ha, or 16%, of the land cover of the study area (Fig. 3.1; SWReGAP data, Lowry et al. 2007), and range in elevation from 2290 m to 2658 m. Average winter temperatures range from -1.4˚C to 0.7˚C and average summer temperatures range from 16.5˚C to 20.0 ˚C. Average winter precipitation ranges from 149 mm to 237 mm and average summer precipitation ranges from 138 mm to 174 mm (1981-2010 PRISM data, accessed January 1, 2014, Daly et al. 2008) for sampled ponderosa pine forests. Piñon-juniper woodlands cover about 54,821 ha, or 37%, of the study area (Fig. 3.1; SWReGAP data, Lowry et al. 2007) and range in elevation from 1876 m to 2479 m. Average winter temperatures range from -1.0˚C to 1.2˚C and average summer temperatures range from 17.5˚C to 22.1˚C. Average winter precipitation ranges from 108 mm to 208 mm and average summer precipitation ranges from 104 mm to 160 mm (1981-2010 PRISM data, accessed January 1, 2014, Daly et al. 2008) for sampled piñon-juniper woodlands.

Historic and current land-use has affected these ecosystems, and present day states are most likely the legacy of past land-use and management activities. Contemporary land-use includes grazing and recreation. Livestock grazing and logging have been major land-use activities historically. Unrestricted grazing in the late 1800's and early 1900's led to overgrazing in many parts of the study area resulting in erosion and altered plant communities in woodlands and forests. During the 1960's and 1970's aerial and rangeland drill seeding treatments for erosion control and range improvement programs were implemented. Exotic grasses were used in these seeding treatments and have led to persistent exotic plant populations and altered plant community dynamics. Crested wheatgrass (*Agropyron cristatum*) was seeded at lower elevations, and Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) were seeded at higher elevations. Additionally, logging in ponderosa pine forests in the 1960's and 1970's has left second growth ponderosa pine stands with oak (*Quercus gambelii*) and greenleaf manzanita (*Arctostaphylos patula*) dominating the understory (USFS, *personal communication*).

Conceptual models of ecosystem dynamics

A priori STMs were developed for each ecosystem of interest to describe the putative states and the general processes most likely to have caused state shifts. These models were based on field observations, relevant literature, and existing STMs in published ecological site descriptions by USDA Natural Resources Conservation Service (https://esis.sc.egov.usda.gov/). Ecosystem dynamics and the related processes depicted in the models provide a resilience based framework for examining the current variability of ecosystems throughout the study area.

Mountain ponderosa pine forests. This model describes the *reference state* and three alternative states for ponderosa pine ecosystems (Fig. 3.2). States are differentiated by overstory tree densities and understory plant community composition that differ in response to fire suppression and grazing (Carpinelli and Gonzalez 2008). State 1, the *reference state*, including community phases 1.1 and 1.2, reflects pre-European dynamics where frequent, low intensity surface fires consumed ground fuels and thinned younger trees maintaining savannah or park-like communities with large old-growth trees (Brown et al. 1999, Moore et al. 1999). State 2,the *current potential state*, including community phases 2.1, *ponderosa pine park*, and 2.2, *at-risk overgrown*, is similar to the *reference state* with the addition of persistent exotic plant populations, mostly perennial grasses such as Kentucky Bluegrass (*Poa pratensis*) or smooth brome (*Bromus inermis*). State 3, *high fuel load*, represents an alternative state resulting from the interacting effects of fire suppression and livestock grazing that have facilitated 1) understory shrubs and younger trees to increase in density and 2) an accumulation of litter and woody debris creating the fuel load and fuel ladder necessary for large stand-replacing fires (Belsky and Blumenthal 1997, Veblen et al. 2000, Schoennagel et al. 2004). Alternative state 4, *dramatically reduced overstory*, depicts the loss of overstory trees as a result of a large stand-replacing fire where the overstory tree canopy has been replaced by oak or mixed montane shrubs

(Brown et al. 1999, Bond et al. 2012). Re-establishment of ponderosa pine forests will naturally happen through succession, but can take 150-years to return to previous states (Komarkova et al. 1988). This timeframe is outside the 20-year timeframe of most management plans (Herrick et al. 2006) so active restoration efforts are required to return these systems to previous states within most management timeframes. The *dramatically reduced overstory* state is considered a terminal state in this model.

Upland piñon-juniper woodlands. This model describes four acknowledged states and the general processes responsible for transitions in piñon-juniper woodlands (Fig. 3.3). The interacting effects of land-use and climate are primary drivers differentiating changes in ecosystem structure and function in these ecosystems (NRCS 2008b, 2008c). State 1, the *reference state* that includes community phases 1.1 and 1.2, represents the historic ecosystem dynamics that are primarily influenced by drought that causes temporary loss of perennial grass and forbs in the understory community (Betancourt et al. 1993, Miller and Wigand 1994). State 2, the *current potential state*, illustrates similar dynamics to the *reference state* with the addition of persistent exotic plants populations (Bashkin et al. 2003). Alternative state 3, *invaded annualized* state, is dominated by persistent annual exotic plant populations, primarily *B. tectorum* or *Salsola* species, often with bare ground in the plant interspaces (Miller and Tausch 2000). This state is often the result of interactions between heavy surface disturbance and drought. Alternative state 4, *eroded state*, is characterized by an increase in plant interspaces and a degraded understory plant community that allows piñon pine (*P. edulis*) and Utah juniper (*J. osteosperma*) densities to increase, resulting in higher than normal canopy closure that inhibits the recovery of understory plants and facilitates large patches of bare ground (Miller and Wigand 1994, Davenport et al. 1998).

Sampling design

Our study substituted space for time and utilized a stratified spatially-balanced random sampling design to determine sampling plot locations that provide inference to the sampled ecosystems. A landscape accessibility model developed by the National Park Service (Garman 2005) was used to remove slopes too steep to safely and efficiently sample (>40%) from the sampling frame. Soil map units from an order-three soil survey (USFS, *unpublished*) were used as the foundation of the sampling frame. To increase sampling efficiency, soil map units dominated by rock outcrops were removed from the sampling frame. The Reversed Random Quadrant Recursive Raster method (Theobald et al. 2007) was used to generate 300 spatially balanced random sampling points in ArcGIS 9.3 (ESRI 2009). Each point was the center of a 1-ha macro-plot consisting of three 50-m transects spaced 25-m apart oriented along the slope contour. To make sure sampling was constrained to a single ecological site, plot centers were adjusted up to 35 m so transects did not cross vegetation, soil, or geomorphic boundaries. The sampling point was rejected if the plot could not be adjusted to accommodate a relatively homogeneous ecosystem.

Field and lab measurements

Plots were sampled from late May to late August 2011 and 2012 to capture adequate vegetation cover (Fig. 3.1). Field measurements were selected to quantify ecosystem structure and function (National Park Service 2003, Herrick et al. 2009). Although other measurements were collected on the plots, only vegetation and soil surface cover, canopy closure, tree density, soil pedon depth, pedon rock fraction and surface soil texture were used in these analyses. Vegetation and soil surface cover was estimated by line-point intercept at 1 m intervals (Herrick et al. 2009). Canopy closure was estimated using a spherical densitometer (Bellow and Nair 2003) at 10 m intervals along each transect. A census of all overstory trees greater than 15-cm diameter at breast height (DBH) in the upper left quadrant of the plot was used to estimate overstory tree densities (National Park Service 2003). Soil pits were hand dug about 10 m downslope of the plot center to describe soil pedon characteristics including pedon depth and rock fraction (Schoeneberger et al. 2002). Surface soil texture was calculated using the hydrometer method (Gee and Bauder 1979) from composite soil samples of the top 10 cm of soil that were collected at five random locations along each transect.

Statistical methods

To increase the utility of the STMs and to increase the inference from the statistical models, similar ecological sites were combined into broad life zone-vegetation type groups (Bestelmeyer et al. 2010). Mountain ponderosa pine forests consisted of 48 plots from mountain loam (n = 34), mountain sandy loam (n = 11), and mountain steep loam (n = 3) ponderosa pine ecological sites (see Chapter 2). Upland piñon-juniper woodlands were composed of 17 plots from upland loam (n = 10), upland steep stony loam (n = 2), and upland stony loam (n = 5) piñon-juniper ecological sites.

State identification. States were identified using Wards hierarchical cluster analysis and nonmetric multidimensional scaling (NMDS) was used to interpret and visualize the clusters (Borcard et al. 2011, Legendre and Legendre 2012) using cluster

1.14.4 (Maechler et al. 2013), pvclust 1.2-2 (Suzuki and Shimodaira 2011), vegan 2.0-10 (Oksanen et al. 2013) packages in R 3.0.2 (R Core Team 2013). The data used to identify states were chosen to describe ecosystem structure and include relative plant species, rock, bare soil, litter, duff, and woody litter cover, and overstory tree density. Bray-Curtis dissimilarity was used to calculate multivariate distance between plots (Legendre and Gallagher 2001).

Wards hierarchical cluster analysis was chosen because it minimizes within-group variance and works well with community data (Borcard et al. 2011). Two statistics will be reported on the efficiency of the cluster analysis: 1) the agglomerative coefficient (AC) measures the structure of the cluster analysis and values closer to 1 indicate more structure, and 2) the cophenetic correlation coefficient (CC) describes the accuracy of cluster analysis and values near 1 indicate higher accuracy (Legendre and Legendre 2012).

NMDS is an unconstrained ordination technique that represents the ordered relationships among objects in reduced ordination space (Legendre and Legendre 2012). NMDS was iterated 100 times or until a stable solution was reached. The stress function measures how far the ranked order is from being monotonic to the original distance matrix and is synonymous to variance. Stress values less than 0.2 indicate a good solution. Indicator species analysis was also used to help interpret the clusters using the indicspecies 1.7.0 package (De Cáceres and Legendre 2009) in R 3.0.2 (R Core Team 2013).

State validation. To validate alternative state groups, canonical correspondence analysis (CCA) was used to test the relationships between ecosystem structure and climate, and ecosystem structure and soil properties using vegan 2.0-10 (Oksanen et al. 2013) in R 3.0.2 (R Core Team 2013). Mean seasonal precipitation and mean seasonal temperature were derived from 800-m 1981 to 2010 normalized Parameter-elevation Relationships on Independent Slopes Model (PRISM) data (Daly et al. 2008) using ClimateWNA software v4.72 (Hamann et al. 2013). Soil properties included pedon depth and rock fraction from the soil pits and soil texture from composite surface soil samples. CCA explicitly examines the relationships between two data sets by testing whether an explanatory matrix (i.e., climate or soil properties in this case) significantly explains the variation in a response matrix (i.e., plant and ground cover, and tree densities; Legendre and Legendre 2012). This would be demonstrated by no clear ordering of the response matrix when the CCA is plotted. Conversely, if climatic or soil properties do explain the variation between states then the differences between ecological sites included in the response matrix is too large to confidently identify states. This would be demonstrated by clear ordering of the response matrix when the CCA is plotted. Because we were interested in ecosystem-level relationships, sample scaling was used to optimize the inter-sample relationships (as opposed to species scaling that optimizes inter-species relationships), and results are illustrated with linear combinations of sample scores in explanatory matrix space. The proportion of variance explained by soil or climatic properties was tested with global Monte Carlo analysis of variance (ANOVAs) of the CCAs with 1000 permutations.

Results

Mountain ponderosa pine forests

Six clusters were identified and described for ponderosa pine ecosystems (Fig. 3.4). Cluster analysis was well-structured (AC = 0.975) and accurate (CC = 0.589). The first two axes of the NMDS explained 91% of the variance of the data (stress = 0.092) and a stable solution was reached in 8 iterations. The first axis was largely composed of overstory ponderosa pine (*P. ponderosa*) density. The second axis was comprised of a combination of overstory *P. edulis* and *J. osteosperma* densities, and *Arctostaphylos patula*, *Petradoria pumila*, *Symphoricarpos* species, *Mahonia repens*, *Elymus elongates*, and duff cover. When environmental variables were fitted to the first two NMDS axes, elevation and soil texture were strongly correlated with the second axis.

Two of the clusters corresponded to community phases and two clusters corresponded to alternative states hypothesized in the *a priori* STM: phases 2.1 *ponderosa pine park* and 2.2 at-risk overgrown, and states 3 *high fuel load* and 4 *dramatically reduced overstory* (Table 3.1, and Figs. 3.2 and 3.4). The differences in ecosystem structure between the ponderosa pine states is the result of prolonged fire suppression. Two of the clusters closely matched ponderosa pine densities and vegetation cover proposed in community phase 2.1, *ponderosa pine park*, and community phase 2.2, *at-risk overgrown*, in the *current potential state*. Following NRCS STM methodology, the existence of persistent exotic plant populations necessitates that this cluster is placed in the *current potential state*. Plots in community phase 2.1, *ponderosa pine park*, have relatively low tree densities (128 trees/ha) and shrub cover (24%), and relatively high perennial grass (27%) and forb (16%) cover (Table 3.1) suggesting that low intensity fires, or other fuels reduction projects, have kept ladder fuels low and maintained an open park-like setting. Relatively moderate tree densities (253 trees/ha) and shrub cover (32%) in community phase 2.2, *at-risk overgrown* (Table 3.1), indicates that recent fire has not occurred at these plots allowing ladder fuels to build up making these areas vulnerable to transitioning to alternative state 3, *high fuel load*. High tree densities (621 trees/ha), and tree (13%) and shrub (32%) cover in alternative state 3, *high fuel load* (Table 3.1), may be high enough to facilitate large stand-replacing fires that could shift these plots to alternative state 4, *dramatically reduced overstory*. Plots in alternative state 4, *dramatically reduced overstory*, lacked overstory trees and had very high shrub cover (60%; Table 3.1). These plots have experienced large stand-replacing fires (Van Scoyoc, *field observations*) and are dominated by oak/mixed montane shrub communities. Some tree recruitment has been observed in these plots, but natural ponderosa pine regeneration could take up to 150 years to return to conditions similar to those in the *current potential state*.

Two clusters that did not fit our *a priori* model were strongly correlated with elevation and soil surface texture. One cluster had high amounts of aspen (*Populus termuloides*) and snowberry (*Symphoricarpos species*) and was positively correlated with elevation and with soils with a high silt fraction; these are considered *upper elevation* plots. The other cluster was associated with high overstory densities of *P. edulis* and *J. osteosperma* and was negatively correlated with elevation and positively correlated with sandier soils; these are considered *lower elevation* plots where piñon-juniper encroachment may be occurring. Although these states are not included in the *a priori* STM, they do represent communities at the upper and lower elevation or climatic limits of the current ponderosa pine distribution. These clusters may be important when considering the response of ponderosa pine communities to climate change. The *upper elevation* plots may be places this community will move toward as conditions warm and dry, and the *lower elevation* plots may represent the front of encroaching piñon-juniper communities as they move up in elevation.

Differences in (1) mean seasonal precipitation (2) mean seasonal temperature, and (3) soil properties did not explain the differences in ecosystem structure, suggesting clusters are true alternative states. (1) Minimal relationship between ecosystem structure and mean seasonal precipitation is illustrated by the lack of distinct order in the CCA plot (Fig. 3.5A). Mean seasonal precipitation explained fifteen percent of the total variation in ecosystem structure and the first two CCA axes explain 95% of this 15%, corresponding to 14.7% of the total variation. The permuted ANOVA indicated precipitation does not explain a significant amount the variance in ecosystem structure ($p = 0.17$). (2) Similarly, a minimal relationship between ecosystem structure and mean seasonal temperature is illustrated by the lack of distinct order in the CCA plot (Fig. 3.5B). Mean seasonal temperature explained 11.5% of the total variation in ecosystem structure and the first two CCA axes explained 11.2% of the total variation. The permuted ANOVA indicated that mean seasonal temperature did not explain a significant amount of the variation in ecosystem structure ($p = 0.48$). (3) Lastly, minimal relationship between ecosystem structure and soil properties is illustrated by the lack of distinct order in the CCA plot (Fig. 3.5C). Soil properties explained eighteen percent of the total variance and the first two CCA axes explained 17.6% of the total variance. The permuted ANOVA indicated that soil characteristics did not explain a significant amount of the variation in ecosystem structure (p = 0.17).

Upland piñon-juniper woodlands

Two clusters were described for upland piñon-juniper woodlands (Fig. 3.6). The cluster analysis was well structured (AC = 0.866) and accurate (CC = 0.640). The first two axes of the NMDS described about 93% of the variance in ecosystem structure (stress = 0.066) and a stable solution was reached after one iteration. The first axis is composed of *J. osteosperma* overstory density. The second was composed of *P. edulis* overstory density and understory cover. Elevation and aspect were strongly correlated with the second axis.

Each cluster corresponded to one of the states in the *a priori* STM (Table 3.1 and Fig.s 3.3 and 3.6). The cluster analysis did not delineate community phases within states for this vegetation type. States in piñon-juniper woodlands were differentiated by tree density, perennial grass, exotic plant, and bare ground cover (Table 3.2) and are most likely the result of repeated disturbances that have altered the plant community and facilitated the loss of soil resources. Plots composing State 2, *current potential*, were characterized by relatively low tree cover (35%), canopy closure (31%), and tree density (789 trees/ha), and relatively high perennial grass (13%), exotic plant (5%), and bare ground cover (19%; Table 3.2) suggesting that these plots may have had little recent disturbance. Again, following NRCS STM methodology, the presence of persistent exotic plant populations necessitates that this cluster is placed in the *current potential* state. Alternative state 4, *eroded*, exhibited relatively higher tree cover (53%), canopy closure

(45%), and tree density (1050 trees/ha), and lower perennial grass (4%), exotic plant (1%), and bare ground cover (9%; Table 3.2) indicating that there has been repeated disturbance events that have caused a reduction in perennial grass and an increase in tree density and canopy closure.

Differences in soil did not explain the variation in ecosystem structure between states. However, differences in climate did appear to explain this variation, indicating there is too much variation among ecological sites to confidently identify alternative states with this approach. State 2, *current potential*, is positively correlated with higher seasonal precipitation indicating that these plots receive more precipitation than those in State 4, *eroded* (Fig. 3.7A). Mean seasonal precipitation explained 71.4% of the total variability in ecosystem structure and the first two CCA axes account for 99.9% of that 71%. The permuted ANOVA indicated seasonal precipitation explains a significant amount of the variance in ecosystem structure (p = 0.005). State 2, *current potential*, plots are negatively correlated with higher seasonal temperatures indicating that these plots receive lower temperatures than plots in State 4, *eroded* (Fig. 3.7B). Mean seasonal temperature explained 57% of the total variation in ecosystem structure, and the first two CCA axes accounted for 99.9% of that 57%. The permuted ANOVA indicated mean seasonal temperatures account for a significant amount of the variance in ecosystem structure (p = 0.006). Little relationship between ecosystem structure and soil properties is illustrated by the lack of distinct order in the CCA plot (Fig. 3.7C). Soil properties explain 10% of the variance in ecosystem structure and the first two CCA axes account for 99.9% of that 10%. The permuted ANOVA indicated that the amount of variation explained by the soil characteristics is not significant (p = 0.81).

Discussion

Our results document the existence of alternative states defined by differences in ecosystem structure. In ponderosa pine forests, there were no relationships between ecosystem structure and climate (i.e., mean seasonal precipitation and mean seasonal temperature) or ecosystem structure and soil properties, indicating that these clusters are true states. However, mean seasonal precipitation and temperature did explain a significant proportion of the variance of piñon-juniper woodlands, which does not suggest that these clusters represent different states. Instead, our data suggest that variation in climate plays a large role in determining the structure of these ecosystems in our study area. The piñon-juniper clusters may actually be different states, but more data (i.e., a larger sample size) are needed to confirm whether this is true or whether these clusters are representing different ecological sites. We do not have adequate site history information to explore the transitions between states and therefore rely on published ESDs and published literature to infer state shifts. We conclude that 1) the states represented by the mountain ponderosa pine clusters reflect changes in ecosystem structure caused by land use, and 2) more data are needed from each of the ecological sites in piñon-juniper woodlands to adequately understand ecosystem dynamics.

The states of ponderosa pine forests in our study area are differentiated by ponderosa pine density and are most likely the result of fire suppression (Moore et al. 1999, Allen et al. 2002, Laughlin et al. 2004). In *reference states* of published ponderosa pine ESDs, grass cover ranges from 15-30%, shrub cover is around 25%, and tree densities range from 50-200/ha (NRCS 2006, 2007, 2008c). Grass and shrub cover, and tree densities in community phase 2.1, *ponderosa pine park*, of State 2, *current potential*, are well within the ranges of the *reference states* and represent relatively open, park-like stands. Decrease in fire frequency and severity from fire suppression has been shown to increase shrub cover and small diameter tree densities, facilitate the accumulation of ground and ladder fuels, and increase stress in mature trees (Schoennagel et al. 2004, Noss et al. 2006). The increase in shrub cover and tree density observed in the plots that compose community phase 2.2, *at-risk overgrown*, suggests these plots are “at-risk” of transitioning to alternative state 3, *high fuel load*. Once a stand is in alternative state 3, costly energy intensive fuels reduction projects may be necessary to return to the *current potential* state (Moore et al. 1999, Allen et al. 2002, Laughlin et al. 2004) and the likelihood of large stand-replacing fires is increased (Noss et al. 2006, Bond et al. 2012). The dominance of scrub oak and/or mixed montane shrubs, reduced grass and forb cover, and minimal stand regeneration often follows severe fire (Andariese and Wallace Covington 1986, Brown et al. 1999, Bond et al. 2012), and has been observed in the plots that make up alternative state 4, *dramatically reduced overstory*.

Difference in climate and geographic location between mountain ponderosa pine forests and upland piñon-juniper woodlands may explain why we were able to confidently identify states in ponderosa pine ecosystems and not in piñon-juniper ecosystems. One explanation could be the differences in climatic heterogeneity where the two vegetation types occur. Ponderosa pine forests in our study area were sampled in a relatively homogeneous climatic zone (123 mm range in precipitation and 21.4˚C range in temperature) compared to piñon-juniper woodlands (136 mm range in precipitation and 23.1˚C range in temperature) in our study area. Upland piñon-juniper woodlands in our study may also be more sensitive to differences in seasonal precipitation and seasonal temperature than mountain ponderosa pine forests. As a result, relatively small climatic differences may have a relatively large influence on these ecosystems. Therefore, it may not be useful to apply these statistical procedures to identify alternative states when ecological sites are combined and there is a wide range of climate variability among the sites, as occurred in our study.

Another explanation is that the geographic locations of ponderosa pine forests in the study area are more homogeneous than the geographic locations of upland piñon-juniper woodlands. Most of the ponderosa pine plots were either on the broad plateau of Elk Ridge on the west side of the study area, or on the long, broad toe slope of the Abajo Mountains on the east side. The upland piñon-juniper plots were sampled on a wide variety of landforms, including canyons, benches, hill slopes, and mesa tops, that were well-distributed spatially across lower elevations of the study area. The statistical procedures used in this study may not be as useful for identifying states and constructing STMs when ecological sites have a wide range of landscape positions and geographic locations.

The resolution of the PRISM climate data may also contribute to the inconclusive results for upland piñon-juniper states. The grid size of 800-m PRISM data used to describe the climate for each plot covers 64 hectares (Daly et al. 2008), whereas a sampling plot was designed to sample one hectare. For ecosystems that occur on more heterogeneous landscapes, finer resolution climate data may be necessary to accurately examine these relationships. Additionally, the algorithms PRISM uses to derive precipitation estimates do not always match climate station data in our area as well as the PRISM temperature estimates (Barry Baker, *personal communication*), and this may affect the relationships that we found between precipitation and ecological structure in piñon-juniper woodlands. Although more accurate climate data would increase the precision of the analysis, it is unlikely it would change the relationships we observed.

Even though we do not have conclusive evidence that the clusters in upland piñon-juniper woodlands are different states of these ecosystems, they do correspond to two of the states, *current potential* and *eroded*, in the *a priori* STM. Piñon-juniper woodlands are affected by the interactions of drought and land-use (Betancourt et al. 1993, Miller and Wigand 1994, Barger et al. 2009). Reference conditions for piñon-juniper woodlands consist of 20-60% grass, 5-30% shrub, and 15-30% tree cover in published ESDs (NRCS 2008b, 2008c). Grass, shrub, and tree cover observed in plots that make up State 2, *current potential*, indicate that these plots are most likely part of an “at-risk” community phase that is close to transitioning to State 4, *eroded*, although the cluster analysis was not able to delineate community phases of piñon-juniper woodlands. Repeated and/or heavy disturbance has been shown to cause soil degradation, declines of understory plant cover, increased bare ground cover, and an increase in canopy closure. These changes facilitate erosion and loss of soil resources that inhibit understory plant community recovery and lead to over-mature trees (Miller and Wigand 1994, Davenport et al. 1998, Redmond et al. 2013). In the plots that make up alternative state 4, *eroded*, low perennial grass cover and high canopy closure, tree cover, and tree density are consistent with over-mature woodlands described in published STMs. However, a decrease in bare ground cover and a similar amount of shrub cover in State 4 plots compared to State 2 plots is not consistent with the amount of erosion and loss of understory vegetation cover described in published STMs. This discrepancy may be due to the differences in ecological sites used in this analysis and not due to alternative states of piñon-juniper woodlands in the study.

Implications for land management

Our strategy began with high-intensity sampling to characterize the ecological structure and function that is present in our study area. Quantitative analytical techniques were used to identify alternative states within similar ecosystems. We concluded by validating the hypothesized states by examining the relationships between ecosystem structure and climate, and ecosystem structure and soil properties. This is not the final stage of identifying and describing alternative states in STMs, however. Several steps outlined by Bestelmeyer et. al. (2009) are still essential to the STM development process. The application of local knowledge cannot be left out before alternative states concepts are finalized (Knapp and Fernandez-Gimenez 2009, Knapp et al. 2010). Next, medium intensity surveys should be conducted to verify and locate alternative states followed by further refinement of the STM concepts (Bestelmeyer et al. 2009, 2010). Lastly, implementation of a monitoring program is recommended, using the existing sampling plots and adding plots in areas of concern (Theobald et al. 2007).

Ecosystem degradation often leads to decreased ecosystem function and decreased ability to provide desired ecosystem services. Montane and upland ecosystems are recognized for providing various ecosystem services such as clean water, clean air, and recreational opportunities. When management practices preserve ecosystem resilience, ecosystems can provide a wider range of these services (Briske et al. 2006). Management strategies benefit from explicit evaluation of existing ecosystem conditions, the breadth of ecosystem services that each can support, and the potential risks and trade-offs associated with alternative management strategies. The application of this approach in areas that do not have published STMs, such as USFS lands, will provide a better understanding of ecosystem dynamics and the response to disturbance, allowing management prescriptions to be adapted in response to shifting ecological conditions.

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Table 3.1. Mean (range, standard deviation) percent plant life form cover and tree density for mountain ponderosa pine forest states.

State	Tree Cover	Shrub Cover	Perennial Grass Cover	Forb Cover	Exotic Plant Cover	Tree Density (per ha)
2.1 Ponderosa Park	7.9 (0-45.6, 12.2)	24.3 (0-78.7, 25.4)	26.8 (0.9-57.8, 16.1)	15.7 (1.5-53.4, 13.9)	13.4 (0-33.3, 11.8)	128 (64-208, 39.2)
2.2 At-Risk Overgrown	6.8 (0-24.1, 6.6)	31.8 (0-82.6, 25)	24 (0-54.5, 16)	11.5 (0-40, 12.6)	9.2 (0-37.3, 10.3)	253 (176-384, 58.5)
3. High Fuel Load	12.6 (0-26.1, 10.2)	31.8 (2.4-56.8, 23.3)	22.6 (2.6-58.3, 21.3)	10.4 (0-24, 9)	13.4 (0-56, 21.1)	621.3 (496-768, 98.8)
4. Reduced Overstory	3.9 (0.6-8.7, 4.3)	59.6 (45.6-76.7, 15.8)	17.6 (6.8-24.7, 9.5)	6 (4-8.2, 2.1)	9.4 (2.3-16.5, 7.1)	0
Lower Elevation	10.1 (4.6-15.9, 5.1)	65.4 (42-82.9, 17.2)	9.8 (0-23.2, 9.7)	4.9 (0-11.5, 5)	0.4 (0-1.4, 0.7)	152 (32-320, 121.5)
Upper Elevation	6.3 (1.9-16.1, 6.6)	21.7 (6.9-36.6, 15.4)	29.9 (8.8-53.9, 18.9)	15 (8.1-25.5, 7.5)	17.4 (4.9-52.9, 23.7)	136 (16-480, 229.5)

Table 3.2. Mean (range, standard deviation) percent plant life form cover, canopy closure, tree density, and bare ground cover for upland piñon-juniper woodland states.

State	Tree Cover	Shrub Cover	Perennial Grass Cover	Annual Grass Cover	Forb Cover	Exotic Plant Cover
State 2. Current Potential	35.1 (17.6-54.2, 10.9)	32.9 (11.4-45.8, 10.7)	13.3 (0-41.8, 13.4)	2.8 (0-17.4, 5.8)	2.9 (0-10.2, 2.9)	4.6 (0-17.8, 6.6)
State 4. Eroded	52.8 (34.7-89.2, 21.4)	32.6 (0-52.8, 20.6)	4.4 (0-10.8, 4.1)	0.5 (0-2.3, 1)	2.4 (0-6.5, 2.4)	0.8 (0-2.3, 1.1)

State	Canopy Closure	Tree Density	Bare Ground Cover
State 2. Current Potential	30.7 (0-84.6, 26.5)	789.3 (320-1568, 373.3)	18.7 (4.9-39.6, 10.8)
State 4. Eroded	45.1 (29.6-82.3, 21.8)	1049.6 (256-2976, 1103.3)	9.2 (0-18.2, 7.5)

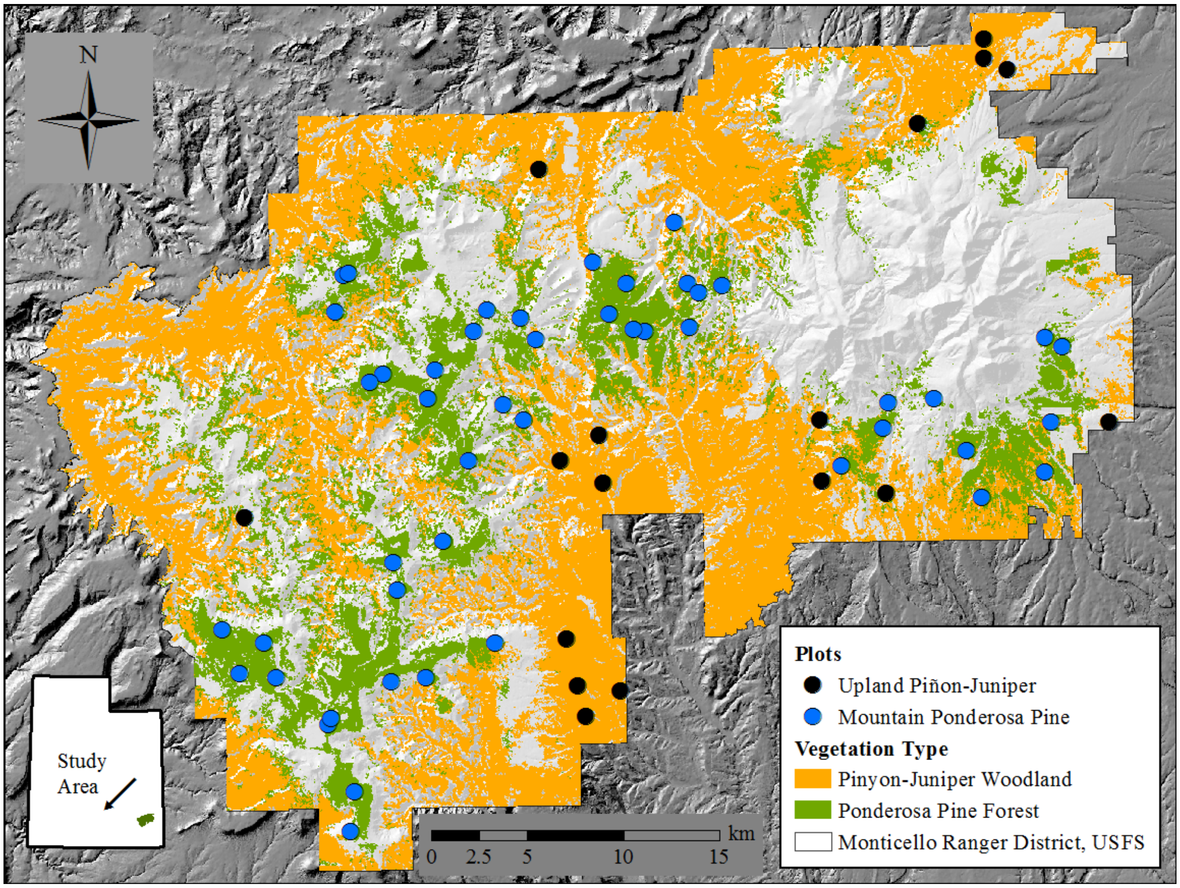
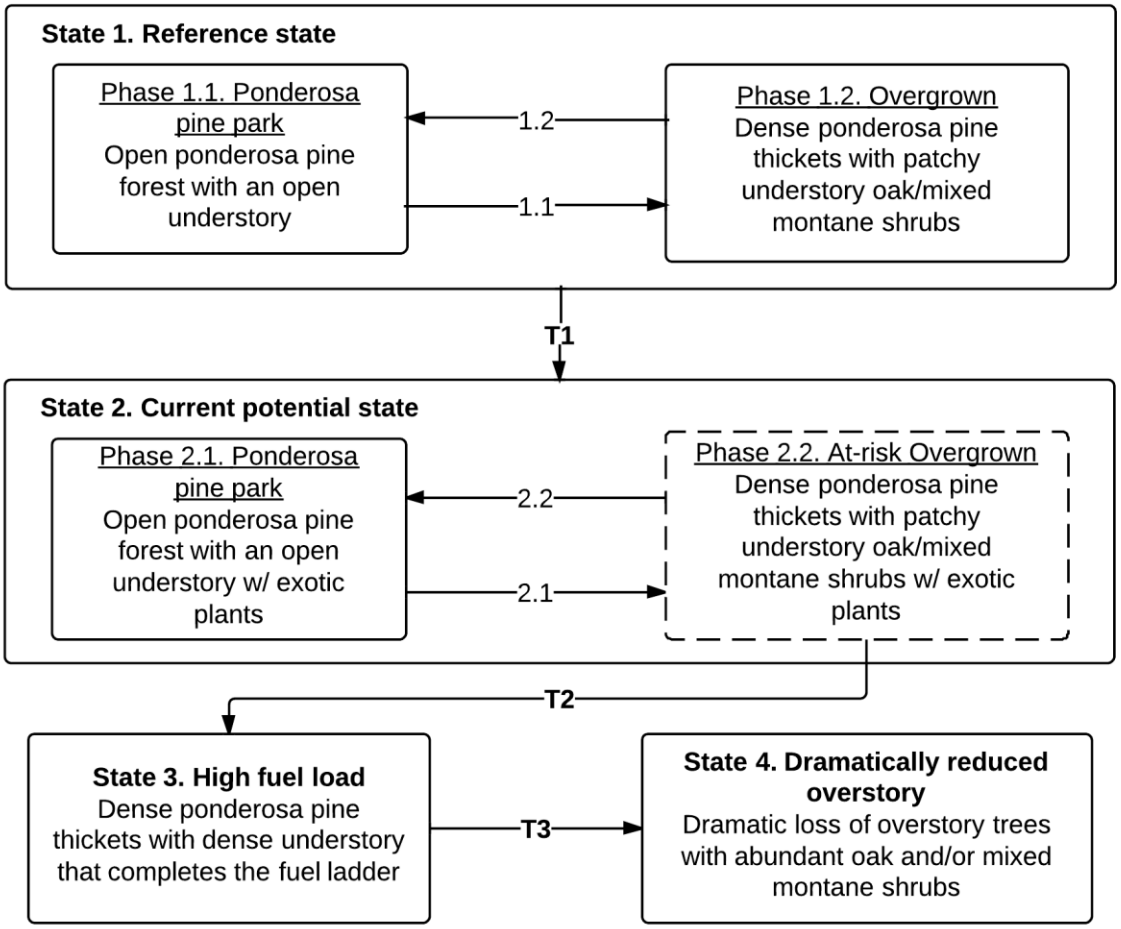


Fig. 3.1. Distribution of ponderosa pine forests and piñon-juniper woodlands and plots sampled in these vegetation types in the Monticello Ranger District, southeast Utah. Vegetation type data is from southwest Regional Gap Analysis Project data (SWReGAP; Lowry et al. 2007) and includes inaccessible areas that were not sampled.



Pathway 1.1: Extended period without fire

Pathway 1.2: Historic low intensity surface fire

Transition 1: Introduction of exotic plants

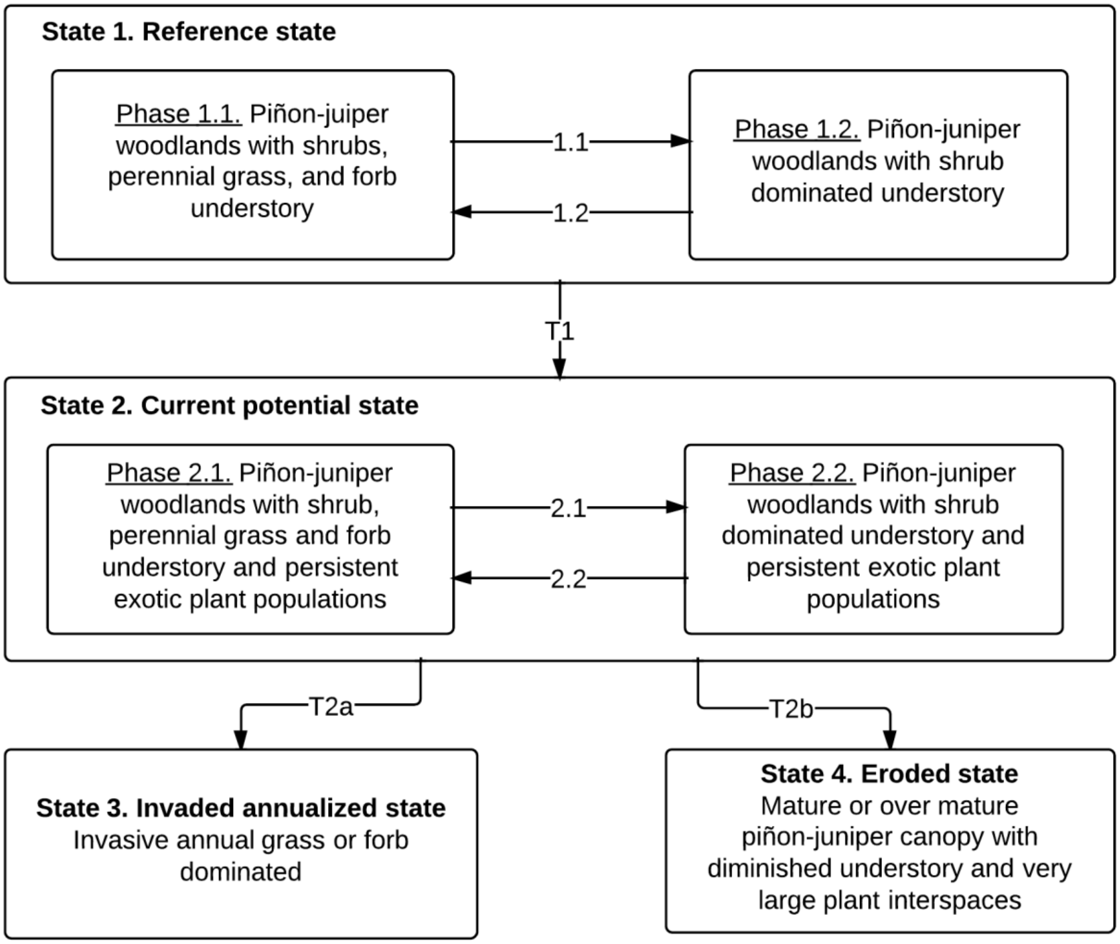
Pathway 2.1: Extended period without fire

Pathway 2.2: Low intensity surface fire

Transition 2: Prolonged fire suppression and heavy grazing resulting in deteriorated understory and increased stand density.

Transition 3: Crown fire or insects infestation resulting in canopy mortality

Fig. 3.2. Conceptual state-and-transition model for ponderosa pine forests. Boxes 1-4 represent ecological states and arrows T1, T2 and T3 represent hypothesized processes responsible for transitions between states. Boxes 1.1, 1.2, 2.1, and 2.2 represent community phases within the *reference* and *current potential states* respectively. The dashed box 2.2 represents an community phase that is vulnerable, or “at-risk”, to transitioning to State 3. Arrows 1.1, 1.2, 2.1 and 2.2 represent pathways between phases respectively.



Pathway 1.1: Prolonged drought causing loss of grasses and forbs

Pathway 1.2: Wetter period allowing grasses and forbs to be abundant

Transition 1: Introduction of exotic plants

Pathway 2.1: Prolonged drought causing loss of grasses and forbs

Pathway 2.2: Wetter period allowing grasses and forbs to be abundant

Transition 2a: Fire return interval allowing exotic annuals to dominate ecosystem dynamics

Transition 2.b: Loss of soil resources and a depleted understory resulting in increased erosion

Fig. 3.3. Conceptual state-and-transition model for piñon-juniper woodlands. Boxes 1-4 represent ecological states and arrows T1, T2a, and T2b represent hypothesized processes responsible for transitions between states. Boxes 1.1, 1.2, 2.1, and 2.2 represent community phases within the *reference* and *current potential states* and arrows 1.1, 1.2, 2.1 and 2.2 represent pathways between phases.

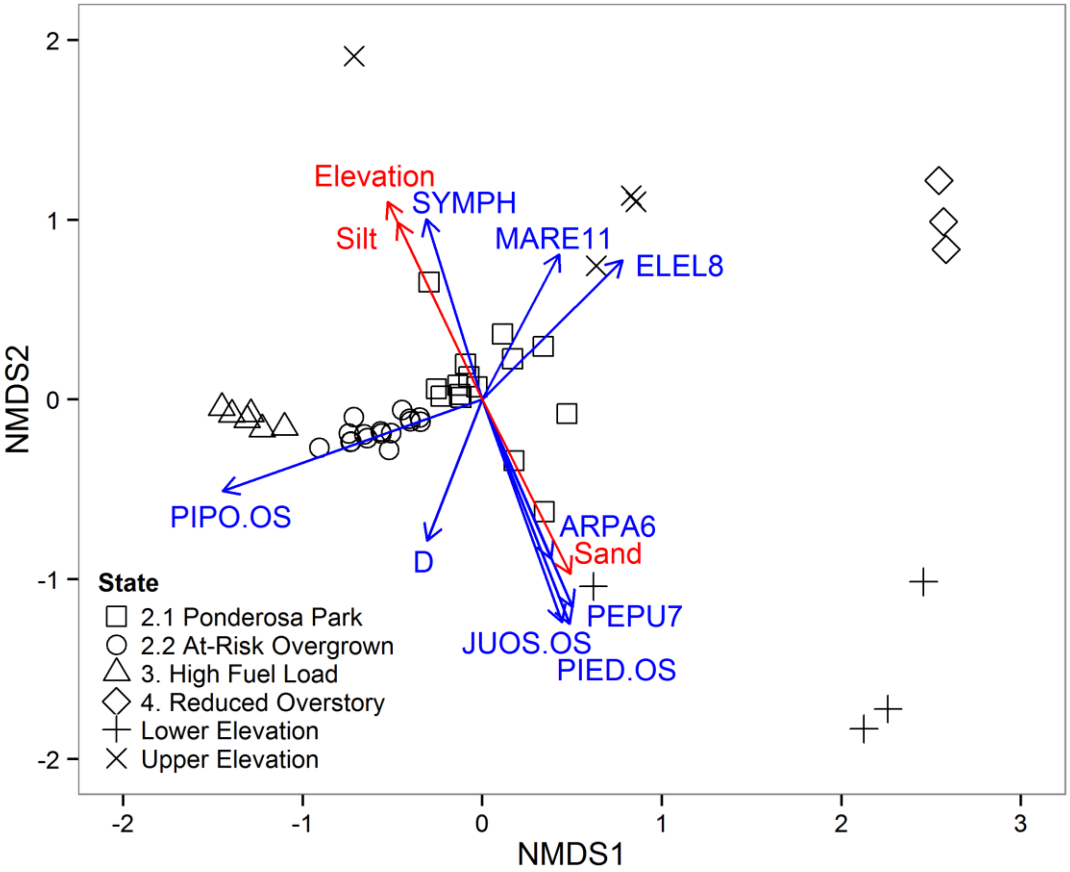


Fig. 3.4. NMDS biplot of vegetation and soil surface cover illustrating clusters derived from hierarchical cluster analysis of ponderosa pine ecosystem structure. Two of the clusters closely match community phases 2.1 and 2.2 and two of the clusters match states 3 and 4 in Fig. 3.2. Two clusters represent communities at the upper and lower elevational bounds of ponderosa pine distribution. Vectors indicate significant vegetation (blue) and environmental (red) properties and length of arrow represents relative significance. Clusters oriented on the left have higher densities of overstory *P. ponderosa* (PIPO.OS). Those toward the top have higher *Symphoricarpos species* (SYMPH), *M. repens* (MARE11), and *E. elongatus* (ELEL8) cover, and are correlated with higher elevation and soils higher in silt. Clusters toward the bottom have higher overstory *P. edulis* (PIED.OS) and *J. osteosperma* (JUOS.OS) densities, and higher *A. patula* (ARPA6), *P. pumila* (PEPU7), and duff (D) cover, and are correlated with lower elevations and sandier soils. The first two axes of the NMDS explained 91% of the variance of ecosystem structure (stress = 0.092).

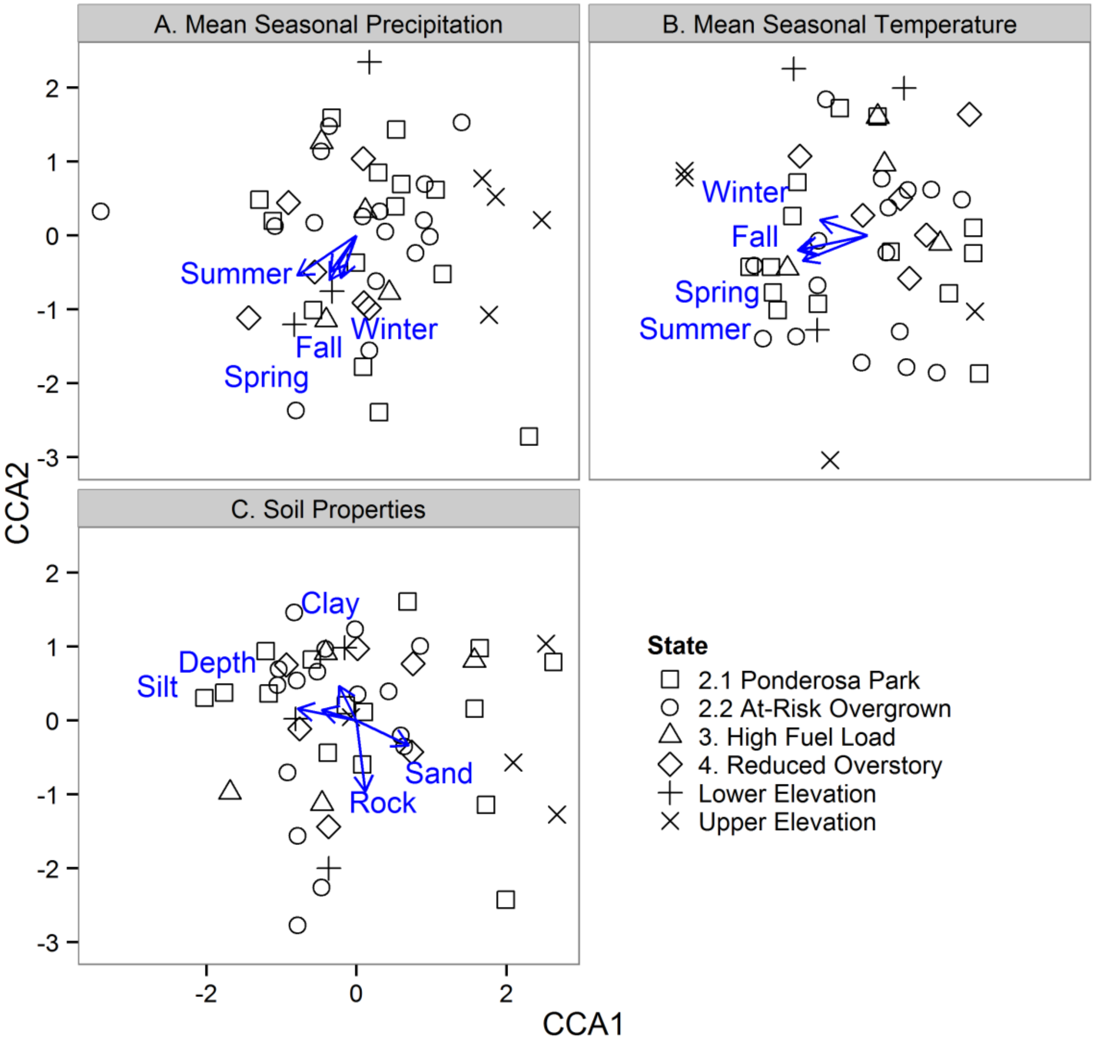


Fig. 3.5. CCA biplots showing relationships between climate and soil properties, and structure of alternative states in ponderosa pine forests. Length of vectors indicates strength of constraining variable. Climate (A and B) and soil properties (C) do not appear to explain the differences in ecosystem structure, suggesting clusters are true alternative states.

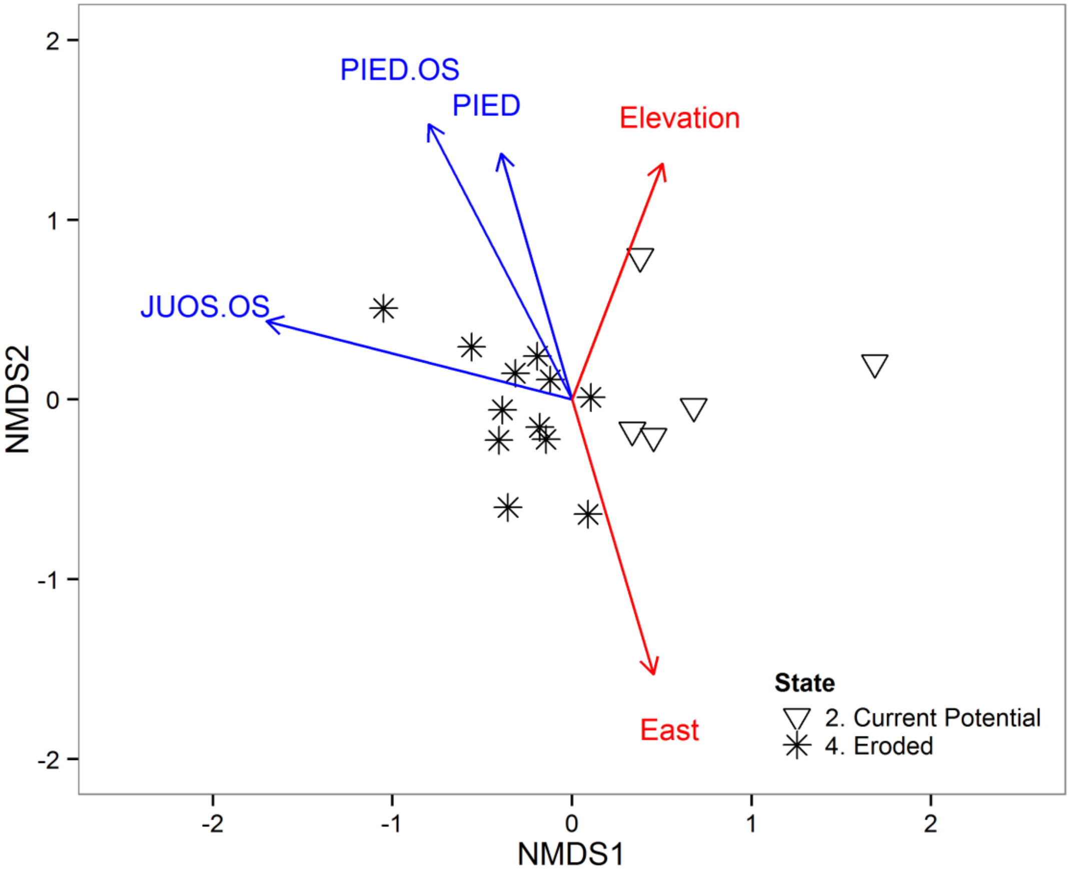


Fig. 3.6. NMDS biplot of vegetation and soil surface cover showing clusters resulting from hierarchical cluster analysis of upland piñon-juniper ecosystems. Both clusters matched hypothesized states in the *a priori* STM (Fig. 3.3). Vectors indicate significant vegetation (blue) and environmental (red) properties and length of arrow represents relative significance. The first two axes of the NMDS explained 93% of the variance in ecosystem structure (stress = 0.066). The first axis is strongly associated with overstory *J. osteosperma* (JUOS.OS) density. The second axis is associated with overstory P. edulis (PIED.OS) density and cover (PIED), and is correlated to elevation and east aspects.

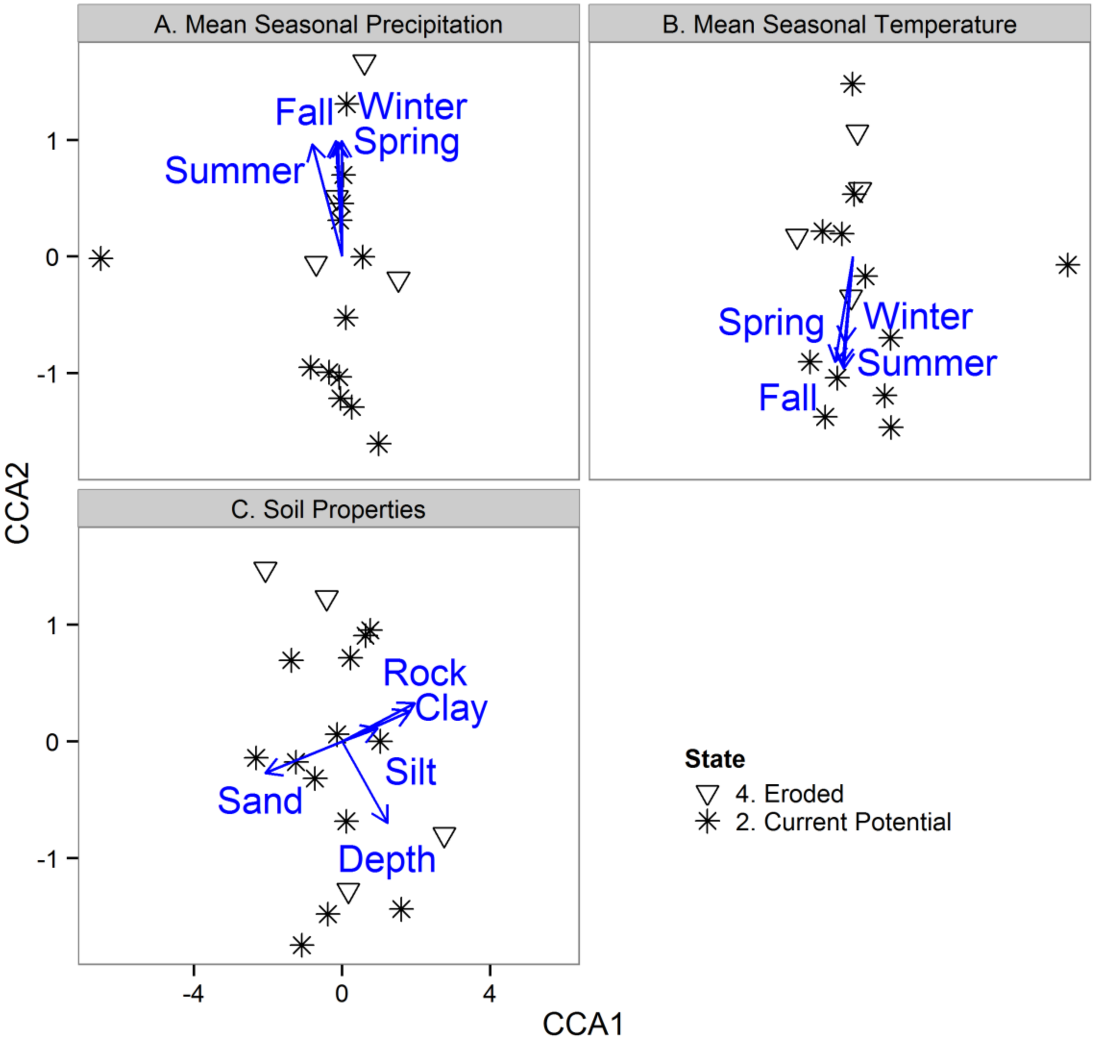


Fig. 3.7. CCA biplot showing relationships between ecosystem structure and climate and soil properties for upland piñon-juniper woodland states. Vector length indicates strength of constraining variable. Differences in climate account for a significant portion of the variation in ecosystem structure, indicating the ecological sites included in this group are not similar enough to each other to confidently identify states. State 2 experiences more precipitation (A) and higher mean seasonal temperatures (B). Soil properties (C) do not explain the variation in ecosystem structure.

CHAPTER 4

CONCLUSION

Changes in land-use and climate are driving ecosystems toward alternative states differentiated by persistent differences in structure and function. Differences between alternative states are important because they affect the types of ecosystem services provided, the potential uses, and the success of management actions (Bestelmeyer and Brown 2010). Landscape classification systems based on ecological potential provide a robust framework for evaluating ecological conditions and alternative states and are important communication tools for understanding ecosystem dynamics and responses to disturbances (Herrick et al. 2006, Brown 2010). State-and-transition models (STMs) are diagrams that depict the multiple stable states that can occur in an ecosystem, and illustrate non-continuous and irreversible ecosystem dynamics between states and continuous and reversible dynamics within states (Stringham et al. 2003, Briske et al. 2005). The ecological site concept, developed by the USDA Natural Resources Conservation Service (NRCS), in conjunction with STMs, uses soil and vegetation characteristics to evaluate ecological properties and have gained popularity with land managers and researchers in recent years. In this study we used data from a large field sampling effort to identify ecological sites and construct STMs on USDA Forest Service land where ecological sites have not been developed. In Chapter 2, we used multivariate statistical procedures to identify ecological sites throughout the study area. In Chapter 3, we developed provisional STMs for mountain ponderosa pine and upland piñon-juniper ecosystems to gain a better understanding of ecosystem dynamics and their response to disturbances.

Ecological sites are not specific locations within a landscape. They are units of a classification system that describe a range of ecological properties, including soil, landform, geologic, and climatic characteristics, and potential plant communities that yield a range of ecosystem processes and services, or ecological potential. Additionally, they represent ecosystem responses to land management actions, and natural and anthropogenic disturbances (Bestelmeyer et al. 2009, Moseley et al. 2010, NRCS 2013). We used hierarchical cluster analysis and non-metric multidimensional scaling (NMDS) ordinations to classified plots based on soils and potential vegetation, delineating and describing statistical ecological site-like groups. Most of our statistical ecological sites matched ecological sites already described by the NRCS. Additionally, we describe one new landscape-soil-vegetation association that has not been described by NRCS as an ecological site in our region, Mountain Sandy Loam (Ponderosa Pine).

STMs are diagrams that illustrate 1) non-continuous and irreversible ecosystem dynamics between states, 2) the continuous and reversible dynamics within states, 3) the mechanisms by which state shifts occur, and 4) the thresholds where changes in soil properties and the plant community prevent recovery to previous states (Bestelmeyer et al. 2004, Briske et al. 2008, Scheffer et al. 2009). We used hierarchical cluster analysis, NMDS, and canonical correspondence analysis (CCA) ordination to examine empirical evidence for alternative states in mountain ponderosa pine (*Pinus ponderosa*) and upland piñon-juniper. Mountain ponderosa pine ecosystem clusters were differentiated by overstory ponderosa pine density and corresponded to three states: *current potential*, *high* *fuel load*, and *reduced overstory*. No relationship was found between ecosystem structure and climate, and ecosystem structure and soil properties, suggesting these clusters are true alternative states of mountain ponderosa pine ecosystem in our study area. Upland piñon-juniper ecosystem clusters were differentiated by overstory Utah juniper (*Juniperus osteosperma*) and piñon pine (*P. edulis*) densities, and plant and bare ground cover that corresponded to two states in the *a priori* STM: *current potential* and *eroded*. The differences in ecosystem structure between proposed states can be explained by climatic differences between the plots indicating too much variability between the upland piñon-juniper ecological sites to confidently identify alternative states. It may be necessary to analyze each ecological site separately to confidently identify alternative states in upland piñon-juniper ecosystems.

The contemporary process used to develop ecological sites and associated STMs is fairly subjective and uses relatively little data to create the ecological site concepts and associated STMs. Utilizing large datasets to identify and describe ecological sites and associated STMs incorporates objectivity into the development process. The alternative methods presented in this thesis are important because 1) they are data driven methods of identifying ecological sites and alternative states and 2) they have the potential to identify new alternative states not conceptualized by the standard methods.

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APPENDIX

Table A1. Indicator species analysis for vegetation type clusters. Species codes are from USDA plants (http://plants.usda.gov/), codes followed by ".OS" are overstory trees.

Species Code	A	B	Pseudo F-statistic	p-value
Aspen				
POTR5.OS	0.99615	1	0.998	0.000999
POTR5	0.811	1	0.901	0.000999
STNE3	0.87757	0.36364	0.565	0.008991
OSDE	0.93567	0.27273	0.505	0.007992
CACA4	0.92915	0.27273	0.503	0.007992
ARCO9	0.9525	0.18182	0.416	0.028971
DAGL	0.81801	0.18182	0.386	0.052947
BETUL	1	0.09091	0.302	0.257742
BOCY	1	0.09091	0.302	0.233766
DENU2	1	0.09091	0.302	0.240759
ELSC4	1	0.09091	0.302	0.233766
GERI	1	0.09091	0.302	0.233766
HYFE	1	0.09091	0.302	0.233766
MAST4	1	0.09091	0.302	0.257742
MEFR2	1	0.09091	0.302	0.233766
MEOF	1	0.09091	0.302	0.232767
POCO	1	0.09091	0.302	0.240759
SARA2	1	0.09091	0.302	0.233766
ACGR.OS	1	0.09091	0.302	0.257742
Mixed conifer				
ABCO	0.7963	1	0.892	0.000999
ABCO.OS	0.9706	0.6	0.763	0.000999
PSME.OS	0.9808	0.4	0.626	0.000999
PSME	0.8448	0.4	0.581	0.003996
AQCO	1	0.2	0.447	0.044955
LEPID	1	0.2	0.447	0.044955
POAR8	1	0.2	0.447	0.048951
SEMU	1	0.2	0.447	0.048951
PIEN.OS	0.9565	0.2	0.437	0.047952
PIEN	0.9465	0.2	0.435	0.045954
SEMU3	0.349	0.2	0.264	0.591409

Species Code	A	B	Pseudo F-statistic	p-value
Grasslands and meadows				
SELA	0.87833	0.27273	0.489	0.00999
HEVI4	0.77929	0.27273	0.461	0.06394
ARLU	0.76722	0.27273	0.457	0.01898
ABLA	1	0.18182	0.426	0.03596
CEAR4	1	0.18182	0.426	0.04096
ABLA.OS	1	0.18182	0.426	0.04396
JUCO6	0.92711	0.18182	0.411	0.04196
ERAL4	0.60575	0.27273	0.406	0.05495
PONI2	0.90675	0.18182	0.406	0.04496
LODI	0.88904	0.18182	0.402	0.07592
ELTR7	0.52238	0.27273	0.377	0.08591
ARDR4	1	0.09091	0.302	0.26773
CLHI	1	0.09091	0.302	0.24376
EQHY	1	0.09091	0.302	0.24476
MALVA	1	0.09091	0.302	0.23277
PHHE2	1	0.09091	0.302	0.28172
POFR4	1	0.09091	0.302	0.24675
POGR9	1	0.09091	0.302	0.24076
POHI6	1	0.09091	0.302	0.26773
LIPE2	0.6558	0.09091	0.244	0.46753
GRSQ	0.59576	0.09091	0.233	0.72428
ARFR4	0.57073	0.09091	0.228	0.61039
Oak/mixed montane shrubs				
SOCA6	0.5514	0.1875	0.322	0.374
LALA3	0.7699	0.125	0.31	0.274
CIRSI	1	0.0625	0.25	0.488
CYMOP2	1	0.0625	0.25	0.472
ELJU	1	0.0625	0.25	0.479
ELLA3	1	0.0625	0.25	0.475
OSOC	1	0.0625	0.25	0.472
ELYMU	0.7251	0.0625	0.213	0.657
CANU3	0.6606	0.0625	0.203	0.796

Species Code	A	B	Pseudo F-statistic	p-value
Piñon pine				
PECE	0.7227	0.3	0.466	0.015
MUMO	1	0.1	0.316	0.109
GIAG	0.9045	0.1	0.301	0.173
Ponderosa pine				
SECR	1	0.075	0.274	0.301
CEFE	1	0.025	0.158	1
CEMA2	1	0.025	0.158	1
PHLOX	1	0.025	0.158	1
PTAQ	1	0.025	0.158	1
SALIX	1	0.025	0.158	1
SOLID	1	0.025	0.158	1
Piñon-juniper				
JUOS	0.87437	0.92308	0.898	0.000999
EPVI	1	0.12821	0.358	0.124875
LERE3	1	0.05128	0.226	0.547453
ARMI4	1	0.02564	0.16	0.749251
ASTER	1	0.02564	0.16	0.746254
OEPA	1	0.02564	0.16	0.746254
OPAU2	1	0.02564	0.16	0.745255
Sagebrush				
HECO26	0.5417	0.3125	0.411	0.153
SPCO	0.9125	0.125	0.338	0.133
ABFR2	1	0.0625	0.25	0.476
ARFE	1	0.0625	0.25	0.476
ERAL	1	0.0625	0.25	0.476
TRDU	1	0.0625	0.25	0.444
ZIPA2	1	0.0625	0.25	0.463
PHHO	0.8971	0.0625	0.237	0.428
PLJA	0.8524	0.0625	0.231	0.606
KOAM	0.8288	0.0625	0.228	0.57
ARNO4	0.7063	0.0625	0.21	0.761

Table A2. Results of indicator species combinations for vegetation types. Species codes are from USDA plants (http://plants.usda.gov/), codes followed by ".OS" are overstory trees.

Species Code	A	B
Aspen		
POTR5	0.811003	1
Mixed conifer		
STJA3	0.515756	1
Grasslands and meadows		
None	NA	NA
Oak/mixed montane shrubs		
POPR+QUGA	0.545707	0.8125
Piñon pine		
POFE+AMELA	0.564517	0.7
ARTR2+LUAR3+POFE	0.536263	0.4
Ponderosa pine		
PIPO.OS	0.596102	1
Piñon-juniper		
None	NA	NA
Sagebrush		
AGCR	0.654755	0.375
ARTR2+PUTR2	0.551981	0.3125
ARTR2+GUSA2	0.505332	0.25