Re-evaluating the Ecological Role of a Keystone Species at the Urban-Wildland Interface

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RE-EVALUATING THE ECOLOGICAL ROLE OF A KEYSTONE SPECIES AT THE
URBAN-WILDLAND INTERFACE

by

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B.S., Tufts University, 2006
M.A., University of Colorado, 2012

A thesis submitted to the
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Re-evaluating the Ecological Role of a Keystone Species at the Urban-Wildland Interface

written by Stower Charles Beals
has been approved for the Department of Ecology and Evolutionary Biology

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Dr. Timothy Seastedt

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Dr. Nichole Barger

Date ___________

The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.
ABSTRACT

Prairie dogs are receiving increased attention from landscape restoration managers as a result of intensified interactions at the urban-wildlife interface. While prairie dogs are regarded as a keystone species in natural grasslands due to their effects on ecosystem function and biodiversity, recent studies at the urban-wildland interface have linked the presence of prairie dogs to unexpected plant compositional changes and the creation of novel plant communities. Due to the link between plant community composition, ecosystem structure, and function, the development of novel communities on prairie dog colonies at the urban-wildland interface suggests the creation of a system highly resilient to restoration efforts with altered ecosystem services. To this aim, my dissertation examines prairie dog colony restoration at the urban-wildland interface by observing changes to plant communities and species following the removal of prairie dogs due to plague epizootics and management intervention. I demonstrate that plague extirpations will not restore plant communities to historical compositions, but rather allow for a potential proliferation of introduced winter active species and exotic forbs. Furthermore, I determine that three years of prairie dog removal will not return plant communities, groups, or vegetation diversity to the levels equivalent to those found on uncolonized areas, and will transition the restored communities to alternative compositions. I also examine the relationship between prairie dogs at the urban-wildland interface and two ecosystem services: wind erosion mitigation and plant productivity, which are both regulated by prairie dogs in a more natural
landscape. My analyses showed nearly ten times the amount of wind erosion emanating from prairie dog colonies at the urban-wildland interface compared to adjacent uncolonized areas, as well as lower forage biomass on colonies than uncolonized grasslands in the region. This research shows that prairie dogs at the urban-wildland interface are operating outside of their historical context, and have the ability to dramatically impact grasslands ranging from plant community compositions to higher level ecosystem services. The ecological role of the prairie dog has changed at the urban-wildland interface, and understanding these changes will be critical for future sustainable management of these valuable grassland areas.
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CHAPTER 1
INTRODUCTION

Background

In the age of the Anthropocene, human impacted landscapes are the new normal. With increasing human development, understanding changes to ecosystems and ecosystem services at the urban-wildland interface will be critical for future landscape sustainability and management decisions (Doak et al. 2013, Wu 2013). In natural prairie landscapes, the presence of black-tailed prairie dogs (*Cynomys ludovicianus*; henceforth prairie dogs) have been classically associated with numerous beneficial ecosystem effects including increased plant community diversity (Bonham and Lerwick 1976, Coppock et al. 1983) and the regulation of ecosystem services such as forage biomass and soil stability (e.g., Holland et al. 1992, Martínez-Estévez et al. 2013). These studies, and other classical research studies (e.g. Detling 1998, Miller et al. 1994, Kotliar et al. 1999) have shaped public and scientific opinion regarding the presence of prairie dogs, and have been used to inform current grassland management decisions. However, recent research conducted at the urban-wildland interface has shown unexpected changes to plant community compositions on prairie dog colonies in heavily anthropogenically-influenced landscapes (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015). These surprising changes, which include increased bare soil exposure, the loss of native grasses, and the proliferation of introduced forbs (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015), suggest that prairie dogs may be operating outside of their historical state at the urban-wildland interface and creating novel plant community compositions (Beals et al. 2014).

Although we have a strong understanding of prairie dogs and colony ecosystems in natural prairie landscapes, the novel colony plant communities at the urban-wildland interface
present unknown restoration challenges, due to their new abiotic conditions and biotic compositions (Hobbs et al. 2009) as well as a disparate surrounding landscape (Suding et al. 2004). While a theoretical framework predicts that restoration of the novel colony communities will not resemble restoration in more natural prairie landscapes (Suding et al. 2004, Hobbs et al. 2009), examples of novel community restoration are highly limited (e.g. Standish et al. 2009). Prairie dog colony restoration has been studied in more natural prairie landscapes (Osborn and Allan 1949, Hartley et al. 2009, Augustine et al. 2014), but the changed ecological role of prairie dogs at the urban-wildland interface suggests that these findings may not be applicable in a heavily anthropogenically-influenced landscape. Understanding the restoration outcome for novel plant communities on prairie dog colonies at the urban-wildland interface will not only contribute a valuable example to novel ecosystem restoration theory, but can directly inform future management decisions thereby improving grassland sustainability.

Due to the link between plant community composition, ecosystem structure, and ecosystem function (e.g. Vitousek et al. 1987, Mack et al. 2001, Ehrenfeld 2003), the plant community shifts observed on colonies at the urban-wildland interface suggest the potential for prairie dogs to additionally alter ecosystem level processes. While the presence of prairie dogs has been linked to regulating numerous ecosystem services in a natural prairie area, including soil stability and forage biomass (Martínez-Estévez et al. 2013), the high levels of bare soil observed on prairie dog colonies at the urban-wildland interface (Beals et al. 2014, Hopson et al. 2015) suggest that colonies may be more vulnerable to aeolian sediment flux than adjacent uncolonized areas. Increased wind erosion on colonies could cause declines in soil fertility, reducing plant biomass (Larney et al. 1994, Larney et al. 1998), and ultimately impacting the long-term sustainability of colonized areas. Understanding the regulating role of prairie dogs for
ecosystem services at the urban-wildland interface will be critical in developing grassland management decisions for the future.

The goal of this dissertation research is to determine the effects of prairie dogs at the urban-wildland interface on plant communities and ecosystem services in order to directly inform future management and restoration decisions. As development in the Western U.S. continues, this research will constitute the groundwork upon which future prairie dog and grassland management policies will be created. Current practices have prairie dog conservation management activities separated from mixed grass prairie conservation activities, which are not sustainable in the long-term. This research will address the current prairie dog knowledge gap at the urban-wildland interface with the hope of informing decisions for successful sustainable management of grassland areas colonized by prairie dogs.

**Research Outline**

The first part of my dissertation research (Chapters 2-3) aims to understand the effects from both passive and active prairie dog removal on novel colony plant communities at the urban-wildland interface. The first research chapter of my dissertation examines the responses of plant communities after prairie dog colony plague extirpations (i.e., passive removal) within the human-impacted landscape of Boulder, Colorado, USA (Chapter 2; Beals et al. 2015). To provide a baseline for comparison and to account for concurrent environmental change, I specifically compared colonies that had recently been extirpated by plague to both areas without prairie dogs and to plague-absent colonies. To include changes in community phenology, my analyses were conducted at three time intervals throughout the growing season and I examined a time period that incorporated one year before the 2005 plague extirpations and six years post
plague. The overall approach utilized remote sensing to quantify changes in the greenness of plant communities for each individual area throughout the study period.

For the second research chapter of my dissertation, my specific aims were to examine changes in species level plant community compositions over three years in response to the removal of prairie dogs (Chapter 3). Prairie dogs were removed from active colony areas with exclosures (i.e., active removal), allowing the plant communities to regenerate for three years without the selective pressure of prairie dog grazing. Grassland areas in the region that are uncolonized by prairie dogs offered a restoration target for this study. Since the timing of a restoration effort can influence the overall outcome, due to climatic factors such as temperature and precipitation, I also examined the temporal effects of prairie dog removal management. I used three main a priori approaches to examine the restoration of the exclosure communities and to evaluate if three years of prairie dog removal returned plant communities to compositions equivalent to nearby reference areas uncolonized by prairie dogs. 1) The restoration trajectory of the exclosure communities was compared to actively grazed prairie dog colonies and nearby grassland areas uncolonized by prairie dogs. 2) I examined the relative cover of different vegetation groups for the different treatments. 3) I quantified and compared the diversity of all, native, and introduced plant species for the different treatment communities.

The second part of my dissertation research (Chapter 4) is focused on prairie dogs regulating ecosystem services at the urban-wildland interface. Due to the increased cover of base soil and plant compositional shifts observed on prairie dog colonies at the urban-wildland interface, there is reason to believe that some ecosystem services regulated by the presence of prairie dogs in natural landscapes are not maintained in a heavily anthropogenically-influenced area. I attempted to test this by examining soil and plant characteristics of prairie dog colonies at
the urban-wildland interface (Chapter 4). I quantified surface soil carbon (C) and nitrogen (N) content from both uncolonized areas and active prairie dog colonies that varied in colonization duration. I also measured aeolian sediment emission rates on and off prairie dog colonies, and examined the C and N content of the wind eroded material. In order to investigate prairie dog colony plant characteristics at the urban-wildland interface, I concurrently quantified the relationship between prairie dog colony age and plant aboveground net primary productivity (ANPP). I believe that the findings of this study will contribute to our understanding of the ecosystem level changes resulting from the presence of prairie dogs at the urban-wildland interface and can be used to inform future long-term sustainable management decision.
CHAPTER 2

RESILIENCE OF A NOVEL ECOSYSTEM AFTER THE LOSS OF A KEYSTONE SPECIES:
PLAGUE EPIZOOTICS AND URBAN PRAIRIE DOG MANAGEMENT


Abstract

In a complex urban-impacted landscape, native black-tailed prairie dogs (*Cynomys ludovicianus*) amplify the trajectory at which grassland plant communities deviate from historical configurations. Prairie dog removal has been proposed as an intervention method based upon the premise that removing a major directional driver of change will initiate the recovery of historically common plant communities. However, in a heavily anthropogenically-influenced landscape with a matrix containing only small fragmented areas of native vegetation, the recolonization speed and success of native plant species may not match those observed in less anthropogenically-influenced landscapes. This study examined the effect of urban prairie dog removal by using remote sensing to observe the response of plant communities near Boulder, Colorado, USA to plague epizootics. We used Mann-Whitney U tests to compare the Soil Adjusted Vegetation Index (SAVI) values from colonies recently extirpated by plague to both areas unoccupied by prairie dogs and to plague-absent colonies. Analysis of 67 Landsat images in three growing season subsets suggested that prairie dog removal alone does not return colony plant communities to compositions representative of grassland areas unoccupied by prairie dogs. The absence of SAVI value changes in the mid- and late-growing seasons suggested that novel vegetation communities on urban prairie dog colonies were highly resilient systems, and prairie dog removal alone was insufficient for restoration. Furthermore, increased early season SAVI values on extirpated colonies could indicate a proliferation of introduced winter active species
and exotic forbs, not the desired reemergence of native species, but rather species expected given current climatic changes. Intensive management efforts appear necessary for overcoming the thresholds required to restore urban prairie dog colonies to their historical compositions, an effort made increasingly more difficult with the ongoing effects of other global change drivers.

**Introduction**

In the age of the Anthropocene, human-impacted landscapes are the new normal. The synergistic effects resulting from biotic (e.g. non-native species introductions) and abiotic directional changes (e.g. changes in climate and land use alterations) are inevitably transforming ecosystems into novel communities with new functions and compositions (e.g. Hobbs et al. 2006). In complex landscapes, the combination of low intensity directional drivers, such as climate change and non-native species invasions, with high intensity events has resulted in rapid community transformations (Scheffer et al. 2012). High-intensity directional change drivers are generally perceived to be major disturbance events, such as droughts and fires, but can also include effects of native keystone species that may be operating outside of their historical state. One such species is the black-tailed prairie dog (*Cynomys ludovicianus*; henceforth prairie dogs). In urban landscapes, prairie dogs can magnify the trajectory of change towards novel plant community compositions at a faster rate than environmental factors acting alone (Beals et al. 2014). As a result of new biotic and abiotic conditions, coupled with the feedback cycles resulting from their synergisms, returning novel systems to their appropriate historical context may require substantial interventions and costly efforts may prove ineffective (Hobbs et al. 2009). Therefore, any empirical evidence that can further our theoretical understanding regarding the effects of directional change drivers on novel ecosystem restoration, as well as directly informing management decisions, is highly valuable for future restoration efforts.
Prairie dogs are receiving increased attention as a result of intensified interactions at the urban-wildlife interface and the desire to return the services and function of degraded grassland ecosystems. Although prairie dogs are generally regarded as a keystone species (Kotliar et al. 1999) in natural grasslands due to their effects on ecosystem function and biodiversity, recent studies have shown that prairie dogs in urban landscapes have elicited unexpected responses including the proliferation of non-native forbs and the loss of perennial native grasses (Magle and Crooks 2008, Beals et al. 2014). The novel plant compositions on urban prairie dog colonies may alter ecosystem processes (e.g. Mack et al. 2001, Ehrenfeld 2003) and dynamics (Vitousek et al. 1987), changing how these ecosystems function, as well as creating a system that retains the same structure, function, and feedbacks (i.e. resilience (Suding and Hobbs 2009, Standish et al. 2014)) despite restoration efforts (Hobbs et al. 2009). Additionally, the presence of urban prairie dogs may decrease ecosystem services by reducing the productivity and cover of native grasses, the primary forage for grazing livestock (Beals et al. 2014). In order to return the ecosystem services and function on urban prairie dog colonies, wildlife managers have proposed prairie dog removal as an intervention method to minimize the expansion of introduced plant species (e.g. City of Boulder Open Space and Mountain Parks 2010); however, the effects of urban prairie dogs, and their removal, on plant communities are poorly understood.

Here we present a study that examines urban prairie dog removal by observing the response of vegetation communities to plague epizootics using remote sensing. *Yersinia pestis*, the causal agent of both bubonic and sylvatic plague, was introduced to the Great Plains in the 1940s (Barnes 1993), and unlike some small mammals, prairie dogs are not naturally resistant to the disease (Barnes 1982). When plague enters a prairie dog colony, it results in mortality rates greater than 95% (Cully and Williams 2001). Studies on plant community changes resulting from
prairie dog removal in natural areas either via plague (Hartley et al. 2009, Augustine et al. 2014) or eradication (Osborn and Allan 1949) suggest that most plant characteristics on plague extirpated colonies were no different from adjacent off colony areas (Hartley et al. 2009), and community recovery can occur less than five years after removal (Augustine et al. 2014). However, previous colony restoration studies (Osborn and Allan 1949, Hartley et al. 2009, Augustine et al. 2014) were conducted in less anthropogenically-influenced landscapes with a matrix dominated by large areas of native plant communities. A heavily anthropogenically-influenced landscape, containing small fragmented areas of native vegetation, may alter native plant recolonization speed and success, with unknown effects on restoration.

In order to return ecosystem function and services, many land managers are willing to undertake drastic measures to restore vegetation communities and prevent the proliferation of non-native species. However, the synergistic effects of the new abiotic and biotic conditions on novel communities can be highly resilient to restoration efforts (Hobbs et al. 2009). In a modern landscape with complex interactions among drivers of change, the removal of a native herbivore is viewed as a restoration option, but the effects of this intervention are unknown. Prairie dog removal due to natural plague epizootics has provided the opportunity to understand and predict the outcome resulting from removal of a directional driver of change as a novel ecosystem intervention effort.

Our specific aim in this study was to examine responses of plant communities after prairie dog colony extirpation within the human-impacted landscape of Boulder, Colorado, USA. To provide a baseline for comparison and to account for concurrent environmental change, we specifically compared colonies that had recently been extirpated by plague to both areas without prairie dogs and to plague-absent colonies. To include changes in community phenology, our
analyses were conducted at three time intervals throughout the growing season and we examined a time period that incorporated one year before the 2005 plague extirpations and six years post plague. Our overall approach utilized remote sensing to quantify changes in the greenness of plant communities for each individual area throughout the study period. Similar approaches have been utilized to examine the effects of grazing pressures on plant community changes (e.g. Bradley and O’Sullivan 2011, Ware et al. 2014) in rangelands similar to those in this study.

**Methods**

*Study Area*

Analyses were conducted within Boulder County, USA, located along the Front Range, east of the Rocky Mountains. This study focused on properties operated by Boulder’s Open Space and Mountain Parks (OSMP), where prairie dogs are protected from development and removal. The landscapes in Boulder County typically occupied by prairie dogs are located within the short and mixed grass prairie ecosystems, but continued development in the region has created a range of anthropogenic pressures surrounding most colonies, such as roads and buildings, and few fragmented areas containing native plant communities (Johnson and Collinge 2004, Beals et al. 2014). Individual prairie dog colony boundaries have been mapped annually by OSMP personnel since 1997. OSMP personnel documented 190 individual colonies on their properties in 2005, with a mean colony area of 7.51 ha and a median area of 1.89 ha (OSMP unpublished data). Colonies examined in this study were located between 40°9’57” and 39°53’32” N and 105°17’20” and 105°7’53” W with an approximate mean elevation of 1645 m. In 2005, prairie dogs occupied approximately 8.2% (1,427 ha) of Boulder OSMP’s total management area (17,395 ha).
Areas of Interest

In order to examine the effect of plague epizootic events on Soil-Adjusted Vegetation Index (SAVI) values and phenology, we selected 20 prairie dog colonies with plague epizootics in 2005 (henceforth plague-present colonies), 17 colonies where plague did not occur from 1997-2011 (henceforth plague-absent colonies), and 21 areas on OSMP properties that do not have a documented history of prairie dog occupation to serve as reference sites (henceforth unoccupied areas; Fig. 1). All prairie dog colonies examined by this analysis were occupied continuously since 2000, providing a sufficient colonization period for prairie dogs to amplify the trajectory of plant community change towards novel compositions (Beals et al. 2014). Ten of the 20 plague-present colonies and six of the 17 plague-absent colonies are located on areas historically tilled for agricultural purposes; however tilling of these areas has not occurred for 15-30+ years (OSMP unpublished data). None of the unoccupied areas have a documented history of tilling. Field observations conducted on the tilled and untilled areas did not observe a legacy effect of the former land use on plant community compositions. In 2004, before the epizootic events, the plague-present and plague-absent colonies had mean areas of 35.50 and 8.88 ha, respectively, while the unoccupied regions had a mean area of 13.24 ha. All areas examined (prairie dog colonies and unoccupied regions) were larger than 1.00 ha in 2005. Smaller areas were not examined due to constraints imposed by the 30 m spatial resolution satellite imagery.

Field observations revealed that the unoccupied areas were dominated by grasses which typically included a combination of native perennial grasses, such as *Andropogon gerardii*, *Bouteloua gracilis*, and *Hesperostipa comata*, with introduced grasses, most commonly *Bromus arvensis* and *Poa pratensis*. In contrast, field observations of the occupied areas revealed that prairie dog colonies in the study areas were forb communities that contained little to no
cover of grasses, and were typically dominated by the non-native forbs *Convolvulus arvensis* and *Erodium cicutarium*. These observed differences in plant community compositions on and off prairie dog colonies in this region are consistent with previous studies documenting plant community changes resulting from the presence of prairie dogs in heavily anthropogenically-influenced landscapes (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015).

The unoccupied areas selected for this analysis had a close proximity to historically active prairie dog colonies (83% of unoccupied areas are within 400 m of a prairie dog colony). Twelve of the 21 unoccupied areas were periodically grazed by cattle as part of OSMP’s grassland management plan. The unoccupied areas were selected based upon their similarities in plant community compositions that we observed during multiple field visits for this study. While properly managed grazing, such as that performed on the 12 unoccupied areas examined by this study, has been shown to typically increase grassland plant community diversity (Olff and Ritchie 1998), we did not observe differences in plant community compositions based on the presence of cattle grazing. Furthermore, the unoccupied areas are all ecologically suitable for prairie dogs; these areas do not contain large cover percentages of trees, riparian corridors, or any other vegetation types that would be unexpected on a prairie dog colony in this region. Multiple field observations have led us to believe that the vegetation communities in the unoccupied areas could represent a successful restoration goal for Boulder County’s urban prairie dog colonies.
Figure 2-1. Locations of plague-present prairie dog colonies (n = 20), plague-absent colonies (n = 17), and unoccupied areas (n = 21) on OSMP properties in Boulder, Colorado (40°0'54" N / 105°16'12" W).

Plague occurrence data

We used time series data from 2005 to 2011 that documented the timing of plague epizootics for each prairie dog colony on OSMP properties in Boulder County. Although plague
epizootics have previously occurred in Boulder County, including numerous events from 1994-1996 (see Collinge et al. 2005), only six epizootics were documented on OSMP properties from 1996-2004. In 2005, there were 77 prairie dog colony epizootics documented on OSMP properties, indicating the start of a new outbreak for Boulder County. While prairie dog colony plague epizootics from the outbreak that began in 2005 have been reported through 2014, the number of documented plague events was highest in 2005, thereby providing the best dataset for this study. Future studies may wish to incorporate extirpation data from additional years into their analyses, but this was outside the scope of this study. From 2005-2014 approximately 33% of the 410 prairie dog colonies on Boulder OSMP properties have had documented plague epizootics, although this number is most likely higher due to undocumented events. As a direct result of epizootics, colony areas reduce dramatically, in some cases by more than 99%, or cause temporary or even permanent extirpations (Cully and Williams 2001, Collinge et al. 2005). OSMP plague occurrence data have been supplemented with personal observations of plague epizootics on OSMP properties.

*Satellite Image Acquisition*

Landsat satellite images were acquired through the USGS EarthExplorer website (earthexplorer.usgs.gov). In order to minimize the error in individual images resulting from atmospheric properties, such as dust and haze, only Landsat Climate Data Record (CDR) Surface Reflectance images were utilized. The Landsat CDR Surface Reflectance images are a level 2A product that have been corrected for atmospheric effects, and are created with the LEDAPS processor (Masek et al. 2006). Since this analysis focused on the typical growing season for Boulder County, all images from March 1st through August 31st that did not contain cloud cover
over the study area were acquired from 2004 to 2011. Images from 2004 were included in order to establish baseline values for all areas before the 2005 plague epizootics occurred. Images with snow present in the study area were not used. In total, we examined 67 surface reflectance images that met these criteria.

*Conversion to Vegetation Index*

Selecting an appropriate vegetation index from the widely utilized approaches, such as the Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI), is essential to any remote sensing study due to the constraints imposed by each index. Field observations and familiarity with prairie dog colonies and OSMP properties in Boulder County suggested that the study areas that we would be examining incorporated vegetation densities ranging from low cover areas dominated by small non-native forbs to higher cover areas with abundant native grasses (see Beals et al. 2014). Due to the expected range of vegetation densities, we chose to utilize the Soil-Adjusted Vegetation Index in an approach similar to Bradley and O’Sullivan (2011). For the SAVI formula:

\[
SAVI = \frac{\rho_{\text{NIR}} - \rho_{\text{red}}}{\rho_{\text{NIR}} + \rho_{\text{red}} + L} \cdot (1 + L)
\]

\(\rho_{\text{NIR}}\) and \(\rho_{\text{red}}\) are the surface reflectance values for Landsat bands 4 (near infrared wavelengths) and 3 (red wavelengths), respectively. \(L\) is an adjustment factor, set to 0.5, the value typically used for intermediate vegetation densities (Huete 1988, Bradley and O’Sullivan 2011). SAVI values range from -1 to 1 with the lower values corresponding to less green vegetation. For each of the 67 surface reflectance images, this conversion process produced a unique image with a SAVI value for each cell in the raster file.
Data Analysis

SAVI values were calculated for each 30 m² raster cell using Python 2.7.3 with the arcpy module (Environmental Systems Research Institute, Redlands, California, USA); an average SAVI value for each area of interest was then extracted. Throughout the study period we used the 2005 colony boundaries for both the plague-present and plague-absent colonies to calculate the mean SAVI value. Although large portions of the 2005 plague-present colonies were not occupied by prairie dogs following the epizootics, records from 2000-2005 indicate that these areas have been recently occupied by prairie dogs and therefore ideal for this study.

In order to examine changes in plant communities throughout the growing season, the 67 images were subset into three categories for the typical growing season: early season (March & April), mid-season (May & June), and late season (July & August). This approach also minimized the effects of precipitation events that occurred days before the satellite images were captured, directly impacting SAVI values. The number of images for each two month growing season period ranged from 1 to 5 with an average of 2.79 images per time period; March & April 2011 was the only time period with one image. Inconsistent availability of imagery can be attributed to cloud cover over the study area. SAVI means for each area were then averaged using all the images in the growing season subset, resulting in one SAVI value for each area for every time period. The SAVI values for March & April 2011 represent the only data available for that year’s early-growing season.

The effect of plague epizootics on colony areas from 2004-2011 was determined with a generalized linear mixed model (GLMM) utilizing the lme4 package (Bates et al. 2012) within the statistical environment R (R Development Core Team, 2011). Colony area values were log
transformed prior to analysis. The use of a GLMM with a Gaussian distribution helped account for the correlation caused by the repeated measures. The model to determine the effect of plague epizootics on colony area included a fixed effect of plague epizootic event (yes or no) and random effects of sample year and individual colony. Plague epizootic event was a binary variable where all plague-present colonies were given a value of 1 following the 2005 epizootics.

In order to examine the effects of plague on SAVI values for each part of the growing season, we conducted comparisons between the plague-present colonies, plague-absent colonies, and the unoccupied areas using non-parametric Mann-Whitney U tests (or Wilcoxon signed-rank tests) in R for each growing season subset every year of the study period.

Additional modeling was performed to determine the factors affecting SAVI values for the plague-present and plague-absent colonies for 2004-2011. Similar to the colony area modeling, analyses were conducted with GLMMs and Gaussian distributions because of the repeated measures caused by sampling the same colonies every year. Our model on SAVI values included fixed effects of plague epizootic event, historic tilling, and colony area. Individual colonies and the sample year were set as random effects. The plague epizootic event variable was utilized following the same approach described in the colony area modeling. The historic tilling of each area was determined from OSMP documentation and modeled as a binary variable (yes or no). Colony area was included in the model because the plague-present colonies did not show a consistent pattern of recolonization after epizootics; furthermore, it was not known what effect the rapid recovery of plague-present colonies would have on SAVI values. In order to compare and evaluate the different model permutations, as well as the relative importance of the individual parameters, we used an information theoretic approach where each model received a relative rank (AIC score) as well as a relative Akaike weight (Burnham and Anderson 2002).
Results

Plague epizootics had a significant effect on prairie dog colony area ($P < 0.001$; Fig. 2). Following plague epizootics in 2005, the areas of the 20 plague-present colonies decreased by 98% from an average of 36.65 ha and a median of 14.92 ha in 2005 to an average of 1.06 ha and a median of 0.05 ha in 2006. Ten of the 20 plague-present colonies were completely expatriated in 2006; however seven of the extirpated areas had been recolonized by 2007. Although recovery of the plague-present colonies was gradual for 18 of the 20 areas from 2006-2011, two out of the twenty plague-present colonies remained extirpated in 2011. In contrast to the plague-present colonies, from 2004-2011 the mean area of the plague-absent colonies fluctuated annually by as much as 26% from the previous year, and ranged from a low of 9.35 ha in 2004 to a maximum of 13.99 ha in 2010.

Fig. 2-2. Plague-present (n = 20) and plague-absent (n = 17) prairie dog colony areas (in ha) from 2004 through 2011. Means ± SE are presented.
Prairie dog removal due to the 2005 plague epizootics increased SAVI values on the plague-present colonies in the early-growing season two years after extirpations, but had less pronounced effects in the mid- and late-growing seasons (Fig. 3). For the early-growing season, there was no significant difference between the SAVI values for the plague-present and plague-absent colonies from 2004-2006 ($P > 0.05$ for all; Fig. 3A); however, plague-present colonies had an average of 13% greater SAVI values than the plague-absent colonies from 2007 through 2011 ($P < 0.05$ for all). Plague-present colonies had significantly lower SAVI values than the unoccupied areas from 2004-2007, as well as from 2009-2011, however, there was no significant difference in SAVI values between plague-present colonies and the unoccupied areas in 2008. In contrast, the plague-absent colonies had an average of 24% less green vegetation than the unoccupied areas from 2004-2011 ($P < 0.05$ for all).

There was no significant difference between the SAVI values on the plague-present and plague-absent colonies values in the mid-growing season from 2004-2011 ($P > 0.05$ for all; Fig. 3B). The amount of green vegetation on the unoccupied areas in the mid-season from 2004-2011 was an average of 23% higher than the values on the plague-present colonies and 21% greater than the values on plague-absent colonies ($P < 0.05$ for all). For the late-growing season, there were no significant differences in SAVI values on the plague-present and plague-absent colonies from 2004-2010 ($P > 0.05$ for all; Fig. 3C); however in July & August 2011, SAVI values were significantly lower on plague-present colonies than plague-absent colonies. Unoccupied area SAVI values were on average 32% greater than the values on plague-present colonies and 29% higher than the values on plague-absent colonies in the late-growing season from 2004-2011 ($P < 0.05$ for all).
Fig. 2-3. Mean SAVI values for plague-present colonies (n = 20), plague-absent colonies (n = 17), and unoccupied areas (n = 21) from 2004–2011 for images from the growing season time subsets of early (A) mid (B) and late (C) growing season. Means ± SE are presented.

Modeling SAVI values for plague-present and plague-absent colonies as a function of colony size, land use history, and the presence of a plague epizootic event for the early-growing
season revealed that the model with the most support included the presence of plague as the lone predictor variable (Table 1). Modeling was not conducted for either the mid- or late-growing seasons because there were no significant differences in SAVI values for the plague-present and plague-absent colonies, with the exception of July & August 2011.

**Table 2-1.** Generalized Linear mixed models of SAVI values for March & April 2004-2011 with fixed effect parameter estimates. Note: *** P < 0.001.

<table>
<thead>
<tr>
<th>Model Predictors of colony SAVI values</th>
<th>Fixed Effect Parameter</th>
<th>Model AICc</th>
<th>Model Akaike Weight</th>
<th>Parameter Estimate</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plague Epizootic</td>
<td>Intercept</td>
<td>0.372 ***</td>
<td>0.022</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Plague Epizootic</td>
<td>0.043 ***</td>
<td>0.009</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>-917.89</td>
<td>0.95</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plague Epizootic &amp; Historic Tilling</td>
<td>Intercept</td>
<td>0.363 ***</td>
<td>0.023</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Plague Epizootic</td>
<td>0.043 ***</td>
<td>0.009</td>
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<td></td>
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<tr>
<td></td>
<td>Historic Tilling</td>
<td>0.021</td>
<td>0.019</td>
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<td></td>
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<tr>
<td></td>
<td></td>
<td>-911.02</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plague Epizootic, Historic Tilling, &amp; Colony Size</td>
<td>Intercept</td>
<td>0.364 ***</td>
<td>0.024</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Plague Epizootic</td>
<td>0.042 ***</td>
<td>0.009</td>
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<td>Historic Tilling</td>
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<td>0.019</td>
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<td>Colony Size</td>
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<tr>
<td></td>
<td></td>
<td>-891.36</td>
<td>0</td>
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</tbody>
</table>

**Discussion**

In complex modern landscapes, the presence of urban prairie dogs has been shown to amplify the trajectory of change towards novel plant community compositions at faster rates than abiotic environmental factors alone (Beals et al. 2014). In order to return the ecosystem function and services historically provided by prairie dog colonies, it is necessary to focus on the restoration of native plant communities once common to colonized areas. Prairie dog removal in a heavily anthropogenically-influenced landscape is a logical intervention effort due to the role of urban prairie dogs as a major directional driver, however the response of novel communities
to losing a driver of change is poorly understood. Naturally occurring plague epizootics in urban prairie dog populations has provided the opportunity to examine the effect of prairie dog removal on novel plant communities. Analysis of satellite imagery acquired throughout the growing season suggests that in a heavily anthropogenically-influenced landscape, prairie dog removal alone does not return colony plant communities to compositions representative of grassland areas unoccupied by prairie dogs within the time span investigated here and in the presence of gradual recolonization of extirpated colonies.

Two years after the 2005 epizootics, the amount of green vegetation increased on plague-present colonies in the early-growing season compared to plague-absent colonies, indicating either a change in early season plant compositions or an increase in plant biomass. However, the differences in SAVI values between the plague-present colonies and the unoccupied areas in the mid- and late-growing seasons does not suggest that plant communities are shifting towards historically common compositions. If prairie dog removal represented the crossing of a restoration threshold by initiating the regrowth of native plants, then we would expect that the SAVI values for the plague-present colonies would be similar to the values observed on the unoccupied areas throughout the entire growing season. Instead, unchanged SAVI values in the mid- and late-growing seasons following prairie dog removal suggests that urban prairie dog colony plant compositions are largely unaffected by prairie dog removal from May through August. The effects of prairie dog removal on SAVI values are unlikely due to the spatial differences between the plague-absent and plague-present colonies because these areas had equivalent SAVI values throughout all growing season subsets in 2004 and 2005, prior to plague epizootics. Despite a lack of response in the mid- and late-growing seasons, green vegetation amounts increased in the early season after plague epizootics, potentially indicating a
proliferation of non-native winter active species and exotic forbs, an observation consistent with local studies (e.g. Prevéy and Seastedt 2014).

Non-native winter active species, such as *Bromus tectorum* and *Erodium cicutarium*, can be successful grassland invaders by growing earlier in the spring than native plants (e.g. Wolkovich and Cleland 2011, Prevéy et al. 2014). Early season growth of non-native winter active species would increase the amount of aboveground green plant biomass, resulting in elevated early season SAVI values, as was observed on the plague-present colonies from 2007-2011. In their study, Prevéy et al. (2014) found that simulated grazing (i.e. mowing) in Northwest Boulder County dramatically increased the cover of introduced winter active species and exotic forbs, most notably *Convolvulus arvensis* and *E. cicutarium*, which have a documented presence on areas occupied by urban prairie dogs throughout Boulder County (Beals et al. 2014). Therefore, the higher early season SAVI values documented on plague-present colonies relative to the plague-absent colonies in 2007-2011 could be caused by the proliferation of non-native winter active species and exotic forbs, such as *B. tectorum*, *C. arvensis*, and *E. cicutarium*, which had been previously controlled by prairie dog grazing. This potential change in vegetation dynamics is particularly interesting since the pattern of higher early season SAVI values following prairie dog removal is maintained throughout the study period despite the gradual recolonization of plague-present colonies.

Plant communities on urban prairie dog colonies were unaffected by prairie dog removal in the mid- and late-growing season and by post-plague recolonization in the early-growing season. Since prairie dogs are well documented drivers of plant community change (Coppock et al. 1983, Detling 1998), we believe the explanation for the lack of SAVI value response to the presence or absence of prairie dogs is the result of a highly resilient ecosystem, rather than an
inappropriate application of remote sensing. Remote sensing has been widely applied with similar approaches to evaluate wetland restoration (e.g. Shuman and Ambrose 2003), vegetation regeneration after fires (e.g. Díaz-Delgado et al. 2003), and measure changes in plant communities (e.g. Washington-Allen et al. 2006, Bradley and O’Sullivan 2011). Furthermore, we believe the increased SAVI values observed in the early-growing season following prairie dog removal is compelling evidence that our methodology is appropriate for this system. One caveat to our methodology is the assumption that all prairie dog colonized areas are fundamentally equivalent to the uncolonized areas, however data were not available to test this assumption. Based on the results of this study, we can effectively surmise that the lack of plant community change could be the result of highly resilient novel systems on urban prairie dog colonies, and the failure of prairie dog removal to overcome thresholds needed to transition the ecosystem to an alternative stable state. While a framework for addressing novel ecosystem restoration thresholds has been proposed (Hobbs et al. 2009, Suding and Hobbs 2009), examples of systems are highly limited (e.g. Standish et al. 2009). Our study contributes a valuable example to this body of literature with a non-invasive low cost approach. We believe that similar successful applications can reduce the implementation of ineffective (and costly) intervention efforts in the future.

Plant communities on extirpated colonies may be unable to return to historic compositions within the time frame investigated because of the abiotic and biotic changes resulting from the presence of urban prairie dogs in a heavily anthropogenically-influenced landscape. Urban prairie dog occupation has been shown to drive plant communities towards novel plant compositions after less than five years of colonization (Beals et al. 2014). In addition to the direct effects of altering plant communities, the presence of urban prairie dogs may also
incorporate indirect effects on colony abiotic processes, such as increased soil temperature, altered hydrologic cycling, and increased soil erosion. As a result of these new abiotic and biotic conditions, as well as their synergistic effects, urban colonies may be unsuitable for native plant recolonization (Yates et al. 2000). The abiotic and biotic conditions on novel ecosystems can be highly resilient to additional change, creating major thresholds for restoration (Hobbs et al. 2009), as seen in the woodlands of Western Australia (Standish et al. 2009). Our findings suggest that removal of the directional driver responsible for amplifying the trajectory of change towards novel compositions (i.e. urban prairie dogs) did not overcome the restoration thresholds of these novel ecosystems and return plant communities to historically common compositions. These results provide further support to the idea proposed by Hobbs et al. (2009) that the restoration of some novel ecosystems could require intensive management strategies or may not be feasible.

Classical restoration from prairie dog grazing demands the recovery of native grasses and the demise of non-native plant species that typically benefit or are relatively unharmed by the presence of prairie dogs (Osborn and Allan 1949, Hartley et al. 2009, Augustine et al. 2014). The seed source driving this recovery can come from either the on-site seed bank or dispersed from adjacent, uncolonized areas. Historically, as well as in previously conducted studies (Osborn and Allan 1949, Hartley et al. 2009, Augustine et al. 2014), prairie dog colonies were in a landscape matrix that was dominated by native vegetation, ungrazed by prairie dog. In these less anthropogenically-influenced landscapes, prairie dog removal due to management intervention or plague epizootics successfully restored plague-present colony plant communities to compositions equivalent to unoccupied areas (Osborn and Allan 1949, Hartley et al. 2009, Augustine et al. 2014). In contrast, colonies within a high-anthropogenic landscape are in a matrix with small fragments, at best, of native vegetation. As a result, the recolonization of native plants on
colonies extirpated by plague epizootics will be a much slower process. Continued spring grazing of seedlings, a behavior observed in the prairie dog colony areas, means that the historical seed bank is slowly being consumed, and the more recent seedlings are more likely to be introduced species (e.g. Bakker et al. 1996). Thus, restoration of urban colony plant communities will be slow at best. Furthermore, the gradual recolonization of urban prairie dog colonies following extirpations results in less recovery time for the colony areas. Collectively, this argues that classical restoration, without strong intervention management activities, is unlikely in a heavily anthropogenically-influenced landscape due to the constraints on the functional role of prairie dogs imposed by the overwhelming anthropogenic impacts.

Modeling approaches to understand the factors affecting SAVI values in the early-growing season revealed that plague presence alone was the best predictor of greenness. Surprisingly, including a predictor variable of historic tilling did not improve the Akaike weight of the model. Historic tilling of areas for agricultural purposes has been shown to change environmental conditions dramatically, often resulting in an increased presence of non-native species (Byers 2002). The lack of historic land use effect on SAVI values for prairie dog colonies suggest that urban prairie dogs may represent a mechanism of directional change that can overcome legacy effects from historic land use. Furthermore, SAVI value independence from historic land use and colony area suggests that any prairie dog colony within the landscape could be susceptible to the observed shifts in vegetation compositions following prairie dog removal.

**Conclusions**

Prairie dog removal has been proposed as a management intervention method in human-impacted landscapes based upon the premise that the removal of a major directional driver will
help restore native plant communities, thereby reestablishing the historical ecosystem function and services of colonized areas. Remote sensing analysis following plague epizootics suggests that prairie dog removal in a heavily anthropogenically-influenced landscape will not restore plant communities to historical compositions found on areas unoccupied by prairie dogs. The lack of change in SAVI values in the mid- and late-growing seasons following plague epizootics suggests that the novel vegetation communities on urban prairie dog colonies are highly resilient systems. Furthermore, changes in early season greenness on colonies where prairie dogs were removed suggests a potential proliferation of introduced winter active species and exotic forbs, not the desired reemergence of native species. While further research should be undertaken to examine plant community changes at the species level, intensive management efforts appear necessary for overcoming the thresholds necessary for restoring these novel communities to some resemblance of the native grasslands that once dominated these areas.
CHAPTER 3

KEYSTONE SPECIES REMOVAL SETS THE RESTORATION OF A NOVEL ECOSYSTEM ON A TRAJECTORY TOWARDS AN ALTERNATIVE STATE


Abstract

Grasslands in the Western US have been lost or degraded due to human impacts, creating a need to preserve and restore existing habitat. Due to the positive ecological role associated with prairie dogs in more natural landscapes, prairie dog conservation management is seen as a potential solution to restore historically common grassland plant communities; however, recent research has shown that the prairie dog’s role is landscape dependent. Prairie dog colonies at the urban-wildland interface have been observed with abiotic and biotic conditions so dramatically different from colonies in more natural landscapes that they have been considered novel communities and present many restoration challenges. In this study, we examined the effect of prairie dog removal, a proposed management intervention effort, in the heavily anthropogenically-influenced landscapes of Boulder and Broomfield Counties, Colorado, USA. Prairie dogs were excluded from active colony areas with exclosures for three years, allowing vegetation to regenerate. Utilizing three main approaches, we evaluated if three years of prairie dog removal returned plant communities to compositions equivalent to nearby reference areas uncolonized by prairie dogs. We used PERMANOVA analyses to observe the restoration trajectory of the exclosure communities relative to both active prairie dog areas and uncolonized areas. Linear mixed models were used to examine changes to the relative cover of different vegetation groups and plant species diversity. Analysis of vegetation compositions, vegetation groups, and plant diversity clearly showed that three years of prairie dog removal did not restore
plant communities to the levels equivalent to those found on areas without prairie dogs. Although 3-5 years of prairie dog removal restored plant communities in more natural areas, the biotic conditions on colonies at the urban-wildland interface, such as plant community compositions and native seed source availability, are likely responsible for making three years of prairie dog removal an ineffective intervention effort in a heavily anthropogenically-influenced landscape. This study demonstrates that restoring novel plant communities by removing prairie dogs is potentially problematic and provides a valuable example to our understanding of novel ecosystem restoration, as well as emphasizing the role and effect of landscape context on ecosystems and restoration.

Introduction

Restoring ecosystems in the 21st century to provide conservation and ecosystem service benefits remains a challenging activity (Higgs et al. 2014). While impacts from some anthropogenic drivers of change, such as non-native species introductions, may take decades to mitigate, the recent focus of conservation efforts on restoring degraded ecosystems has demonstrated that management interventions can be successful (e.g., Suding 2011). However, the more the abiotic and biotic conditions of an ecosystem depart from the historically common levels, the more challenging it becomes to return the ecosystem back to the desired historical state (Hobbs et al. 2009, Hobbs et al. 2014). Novel ecosystems may contain conditions so disparate from their natural counterparts that no natural analogs exist, and therefore present the largest obstacles for a successful restoration (Hobbs et al. 2009, Suding and Hobbs 2009). Despite the challenges, focusing on restoration of novel ecosystems is sometimes essential in order to return the function and services that these areas historically provided.
Black-tailed prairie dogs (*Cynomys ludovicianus*; henceforth “prairie dogs”) are a colonially living herbivore native to the Great Plains of North America. Prior to European settlement, the Western U.S. landscape was a matrix of grassland habitat and prairie dog colonies. Although still very common, prairie dogs once occupied an estimated 10 – 40 million ha in North America in the early 1900s (Miller et al. 2007), and played a valuable ecological role in the grasslands they inhabited (e.g., Bonham and Lerwick 1976, Coppock et al. 1983, Miller et al. 1994). During this time period, the short and mixed prairie grasslands uncolonized by prairie dogs were dominated by native perennial grasses, such as *Boutelous gracilis* and *Pascopyrum smithii* (Larson and Whitman 1942). Although prairie dog occupation increases the cover of native forbs and reduce grasses over time (e.g., Larson and Whitman 1942, Archer et al. 1987), a 3-5 year absence in prairie dogs can shift colony plant compositions back to grass dominated communities that are equivalent to uncolonized reference areas in native prairie systems (Hartley et al. 2009, Augustine et al. 2014). However, more than 150 years of human development has changed the grassland landscape through habitat loss, fragmentation, modified grazing regimes and fire frequencies, as well as altered atmospheric chemistry (e.g., Archer and Predick 2008, Ceballos et al. 2010). The surviving remnant grassland ecosystems can be degraded as a result of non-native species introductions (e.g., Sheley and Petroff 1999, LeJeune et al. 2006) and changes in climate (e.g., Prevéy and Seastedt 2014), and many grassland areas currently exist as fragments within a landscape matrix of anthropogenic features. Since it is not possible to recapture the grasslands lost to development, the remaining option is to restore the degraded areas to the historically common compositions in order to maintain the ecosystem function and services the grassland areas have provided (e.g., Miller et al. 1994, Kotliar et al. 1999).
In the early 1900s, prairie dogs were publically viewed as agricultural pests that threatened livestock ranching, leading to their widespread extermination (Merriman 1902). Starting in the 1960s, research studies began to reveal the valuable ecological role that prairie dogs play in grassland ecosystems, such as increasing colony plant community richness and diversity (Bonham and Lerwick 1976, Coppock et al. 1983), and increasing habitat for macro-invertebrates and rare vertebrates (Miller et al. 1994). Due in part to a changed public perception, prairie dogs are currently considered a conservation objective for many public areas in the Western U.S., since they are a native keystone species (Kotliar et al. 1999) considered by some to be threatened due to habitat alterations, intentional culling by humans, and introduced bubonic plague (Miller et al. 1994). Based upon the foundation of knowledge that has linked numerous positive ecosystem effects to the presence of prairie dogs, many land managers currently view prairie dog conservation as one solution to maintain or restore grassland plant communities, as well as the ecosystem services and function that areas occupied by prairie dogs have historically provided. However, recent research has shown that the ecological role of prairie dogs may change with landscape context and some of those benefits may no longer be associated with their presence (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015).

The foundation of our knowledge on the positive ecosystem effects of prairie dogs comes from research conducted in less anthropogenically-influenced landscapes, such as Wind Cave National Park in South Dakota and the Pawnee National Grassland in Colorado (e.g., Whicker and Detling 1988, Hartley et al. 2009). While these studies are critical in developing our understanding regarding the ecological role of prairie dogs, most communities looking to restore degraded grassland ecosystems are located within landscapes that do not resemble Wind Cave National Park, but instead exist at the urban-wildland interface with numerous anthropogenic
features, such as roads and buildings. Recent studies in these heavily anthropogenically-influenced landscapes have shown that the presence of prairie dogs is linked to unexpected plant community changes, which include increased bare soil exposure, the loss of native grasses, and the proliferation of introduced forbs (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015). The observed plant community changes on colonies in heavily anthropogenically-influenced landscapes are believed to result from high population densities and subsequent overgrazing on prairie dog colonies, caused by both a lack of predator access and the inability of prairie dogs to disperse across anthropogenic features (Johnson and Collinge 2004). Due to the dramatic departure from historical compositions, and the fact that a natural analog did not exist, Beals et al. (2014) proposed that prairie dog colony plant communities in heavily anthropogenically-influenced landscapes represent novel compositions. Following this recognition, there has been little research to further our understanding regarding the new functional role of prairie dogs in heavily anthropogenically-influenced landscapes, the potential consequences resulting from their presence, and ability to restore the novel plant communities on colonies to historically common compositions.

Continued human development has reduced, degraded, and fragmented grassland habitat, as well as introduced new anthropogenic features surrounding prairie dog colonies, and increased interactions at the urban-wildland interface. If the presence of prairie dogs at the urban-wildland interface continues to elicit departures from historical grassland compositions by producing proliferations of non-native species and reducing the presence of native grasses, as the recent research suggests (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015), there could be dramatic changes to plant communities on public lands colonized by prairie dogs with unknown consequences for ecosystem level processes, function, and services. Therefore, in order to
preserve or return the historical function of native grasslands at the urban-wildland interface, the restoration of novel plant communities on prairie dog colonies at the urban-wildland interface is necessary and will become an essential tool for landscape managers. However, because prairie dog colonies in heavily anthropogenically-influenced landscapes contain novel plant communities, it is challenging to predict the outcome of restoration efforts. Currently, over a million people co-occupy municipalities with prairie dogs, so understanding the ecological role of prairie dogs and the consequences of their management is of great importance.

Restoring highly degraded or novel ecosystems poses substantial challenges. In addition to greatly altering plant compositions, the increased bare soil cover observed on colonies in heavily anthropogenically-influenced landscapes may affect abiotic conditions as well, by increasing soil temperatures and changing hydrologic cycling (Archer and Detling 1986) and increasing dust erosion (Seastedt et al. 2013). Furthermore, directional changes to climate and the atmosphere, such as increased mean temperature, expanded growing season length, and increased levels of CO₂ and nitrogen deposition, may be producing abiotic environmental conditions on colonies that have not been experienced in past decades. Due to the altered abiotic conditions and biotic communities on and around prairie dog colonies in heavily anthropogenically-influenced landscapes, and the feedbacks resulting from their synergistic effects, returning historically common plant communities on prairie dog colonies may require intensive or unusual management efforts (Hobbs et al. 2009). In addition to presenting restoration challenges, the feedback dynamics from the new abiotic and biotic conditions of colonies may shift the system targeted for restoration to an alternative state on a trajectory unaligned with the restoration goal (Suding et al. 2004).
Here we present a study that examines prairie dog colony plant community restoration in a heavily anthropogenically-influenced landscape by observing vegetation changes over time in areas where prairie dogs have been excluded. Prairie dog removal has been proposed as a restoration intervention effort by land managers at the urban-wildland interface to reduce non-native vegetation proliferations and return native plant communities (e.g., Boulder County Parks and Open Space 2012), and therefore represents a realistic management approach. Removing the selective grazing pressures created by prairie dogs will allow vegetation to regenerate on colonies, and could result in the management goal of reestablishing the vegetation compositions found on similar grassland areas uncolonized by prairie dogs. Areas uncolonized by prairie dogs typically contain a greater cover of native grasses and less introduced forb cover than are found on colonies in heavily anthropogenically-influenced landscapes (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015). However, restoring historically common plant communities is dependent upon the composition of grazing-tolerant species and native seed source availability (Suding et al. 2004). Due to a landscape matrix of numerous anthropogenic features, native vegetation may exist only as small fragments at the urban-wildland interface, possibly changing the speed and success of native plant regeneration. Climate conditions, such as precipitation and temperature, during the restoration interval are also clearly important (e.g. Holmgren and Scheffer 2001, Harris et al. 2006, Hao et al. 2014).

The new abiotic conditions and biotic communities present on and around prairie dog colonies in heavily anthropogenically-influenced landscapes suggest that the restoration trajectory and dynamics will not resemble those found on colonies in more natural landscapes (Suding et al. 2004, Hobbs et al. 2009), however, since so few studies on prairie dogs at the urban-wildland interface have been conducted, many land managers and the public may not
understand the effect of landscape context on the ecological role of prairie dogs. In one recent study utilizing remote sensing, the novel plant communities on prairie dog colonies in a heavily anthropogenically-influenced landscape showed resilience to short-term extirpations caused by plague epizootics and did not reestablish plant communities resembling areas uncolonized by prairie dogs (Beals et al. 2015). The findings of Beals et al. (2015) support the theory that restoring novel communities through prairie dog removal poses substantial challenges (e.g., Suding et al. 2004, Hobbs et al. 2009); however analysis of prairie dog colony plant community restoration is needed at both the plant species and community levels. Therefore, new research is necessary to inform proper collective management of both grasslands and prairie dogs at the urban-wildland interface.

Our specific aims in this study were to examine changes in species level plant community compositions over three years in response to the removal of prairie dogs within the heavily anthropogenically-influenced landscape of Boulder and Broomfield Counties, Colorado, USA. Prairie dogs were removed from active colony areas with exclosures, allowing the plant communities to regenerate for three years without the selective pressure of prairie dog grazing. Grassland areas in the region that are uncolonized by prairie dogs offered a restoration target for this study. Unlike the prairie dog colonies, uncolonized areas typically have a 20-25% cover of native grasses, 5-10% cover of introduced forbs, and 5-10% cover of bare soil (Beals et al. 2014). Since the timing of a restoration effort can influence the overall outcome, due to climatic factors such as temperature and precipitation, we also examined the temporal effects of prairie dog removal management. We used three main a priori approaches to examine the restoration of our exclosure communities and to evaluate if three years of prairie dog removal returned plant communities to compositions equivalent to nearby reference areas uncolonized by prairie dogs.
1) The restoration trajectory of the exclosure communities was compared to actively grazed prairie dog colonies and nearby grassland areas uncolonized by prairie dogs. 2) We examined the relative cover of different vegetation groups for the different treatments. 3) We quantified and compared the diversity of all, native, and introduced plant species for the different treatment communities. This research will provide insight into the theory of novel community restoration, as well as directly inform grassland and prairie dog management at the urban-wildland interface, an issue that will continue to become more critical with human development.

**Methods**

**Study Area**

All data were collected within Boulder and Broomfield Counties, Colorado, USA. This work focuses on public lands managed by City of Boulder Open Space and Mountain Parks (OSMP) and Broomfield Open Space. Historically, the region’s prairie dogs established colonies within the short and mixed-grass prairie ecosystems that were common in the study area. However, continuous development in the Foothills of the Rocky Mountains since the 1850s has resulted in a complex matrix of anthropogenic features, such as buildings and roads, surrounding the public lands colonized by prairie dogs (Johnson and Collinge 2004). All prairie dog colonies examined by this work were located between 40°9’57” and 39°53’32” N and 105°17’20” and 105°5’15” W with an approximate mean elevation of 1645 m. The average temperature from June-August was 23.36°C in 2012, 21.91°C in 2013, and 20.66°C in 2014. In 2012, there was a total of 14.55 cm of precipitation from June-August, 7.72 cm in 2013, and 17.81 cm in 2014.

*Prairie Dog Exclosures*
In order to examine changes to plant community compositions following prairie dog exclusion, fifteen 2.25 m$^2$ exclosures were established on five prairie dog colonies in March 2012 (three exclosures per site). An additional 12 exclosures were added in March 2013, adjacent to each of the 2012 exclosures, to observe the potential temporal effects on plant community changes. A second set of exclosures was not added to one site due to consideration for neighboring residents. All prairie dog exclosures were established in the active areas of colonies, more than 25 m from the colony edge. Four of the five colonies with exclosures were older than ten years in 2012 and greater than 10 ha in area. None of the colonies with prairie dog exclosures had a known history of agricultural tilling or were actively grazed by livestock. The prairie dog exclosures were constructed with wood framing staked to the ground that was surrounded with 1 m high metal poultry netting to prevent prairie dog grazing but allow access to mice and invertebrate herbivores. The poultry netting extended outward over the ground from the exclosure to prevent prairie dogs from tunneling into the exclosure.

Table 3-1. The number of plots sampled by exclosure treatment during each year of the study. Plant community sampling occurred once a month from June – August in 2012-2014.

<table>
<thead>
<tr>
<th>Year</th>
<th>Actively Grazed</th>
<th>Exclosure Year 1</th>
<th>Exclosure Year 2</th>
<th>Exclosure Year 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td>45</td>
<td>45</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2013</td>
<td>45</td>
<td>36</td>
<td>45</td>
<td>0</td>
</tr>
<tr>
<td>2014</td>
<td>36</td>
<td>0</td>
<td>36</td>
<td>45</td>
</tr>
<tr>
<td>Total N</td>
<td>126</td>
<td>81</td>
<td>81</td>
<td>45</td>
</tr>
</tbody>
</table>

Exclosure Vegetation Sampling

From 2012-2014 species composition surveys were conducted once a month from June through August. Monthly surveys consisted of quantifying the composition of each exclosure plot as well as three plots per site that were adjacent to the permanent exclosures but open to prairie dog grazing. Exclosure plots were labelled based on the age of the exclosure (Table 3-1),
while the plots outside the exclosures were designated as “active prairie dogs.” As a result of a plague epizootic on one colony in the spring of 2014, the active prairie dog plots on the partially extirpated site were not sampled in the 2014 growing season due to decreased prairie dog grazing.

Species compositions were conducted using point-intercept surveys with a 1 m² quadrat frame centered within the 2.25 m² exclosure to minimize the edge effects of the exclosure structure. The quadrat frame contained a 10 x 10 cm grid for a total of 100 sample points per plot, and was aligned to corner markers for each plot to ensure comparability in data across time. All plants under the points were identified to species, and any other hits (bare soil, litter, or rock) were recorded. All data were converted to relative cover prior to analysis.

Colonized and Uncolonized Transect Vegetation Sampling

In addition to the exclosure vegetation sampling, this study used data collected in the City of Boulder during the study period from transects conducted on areas both colonized (i.e. prairie dogs present) and uncolonized by prairie dogs. We utilized the uncolonized transects as a reference dataset for the exclosure plant communities, and examined the effect of vegetation sampling methodology on community compositions with the colonized data. The vegetation data from 13 transects colonized by prairie dogs and 77 uncolonized transects were collected from June through August in 2012-2014 by OSMP personnel. The 77 uncolonized transects were only sampled once during the study period; 27 transects were sampled in 2012, 26 in 2013, and 24 in 2014. The locations of all 90 OSMP transects were randomly selected with a stratified Generalized Random Tessellation System (Stevens and Olsen 2004). Prairie dog occupation of transects was determined in ArcGIS 10.2 (ESRI, Redlands, CA), and verified with OSMP
personnel field notes. Individual prairie dog colonies on OSMP properties have been mapped annually since 1997; therefore it was possible to determine the occupation history of each vegetation transect by examining colony extents relative to transect locations. All colonized transects analyzed in this study were occupied continuously by prairie dogs from 2005-2014. All uncolonized transects had no documented history of prairie dog occupation from 1997-2014, but it is likely that these areas were occupied historically.

OSMP conducted 50 m line point intercept surveys with data collected one meter to the left and right of each 50 m transect line for a total of 100 points (for more detail see Beals et al. 2014). All vegetation and non-vegetation were conventionally classified (Winkworth et al. 1962) with vegetation identified by species, and non-vegetation categorized as bare soil, litter, or rock. Only species included in crosshair ‘hits’ were used for cover data and Shannon-Weiner diversity values. Similar to the exclosure vegetation data, the OSMP vegetation transect data were converted to relative cover prior to analysis. For all vegetation data, plant scientific names, origins (introduced or native), and functional groups (forb, grass, shrub, etc.), reported here follow nomenclature used by the USDA Plants Database (www.plants.usda.gov).

Data Analysis

In order to examine the effects of vegetation sampling methodology on the colonized and active prairie dog plant communities, we used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity among plots with the vegan package (Oksanen et al. 2013) within the statistical environment R (R Development Core Team 2008). In order to test for significant clustering of Bray-Curtis values, we used Permutational Multivariate Analysis of Variance (PERMANOVA) with Bray-Curtis distance matrices in R with the adonis function
from the vegan package. In our sampling design we measured multiple plots within the same site for multiple months per year, however more than one random effect (i.e. sampling year, site, and sampling month) cannot be accurately incorporated into an analysis of community data. Therefore, in order to quantify the effects resulting from different sampling methodology, we only used community data sampled during the month of August and separated each treatment based on the sampling year (e.g. Active Prairie Dogs - 2012). Although using only August data may underestimate the presence of early season plants that could senesce before the end of the growing season, we felt that August best represented the accumulation of growth for the entire summer. To account for the error caused by sampling multiple plots within the same site, we used the site ID number as the group with which to constrain the PERMANOVA analysis and only compared colonized and active prairie dog communities that were sampled in the same year.

We used a similar approach to describe the differences in plant communities between the uncolonized (reference) transects, active prairie dog plots, exclosure year 1 plots, exclosure year 2 plots, and exclosure year 3 plots. Due to the potential temporal effects on community compositions, the exclosure treatments were separated based on the year they were established (i.e. 2012 vs. 2013) in addition the exclosure age (i.e. year 1, year 2, or year 3). Similar to the colonized vs. active prairie dog plot analysis, we used NMDS based on Bray-Curtis dissimilarity among treatments, and quantified differences with the PERMANOVA function in R. Due to the re-occurring issue of multiple random effects inherent in the sampling design, only August sampling data was used and comparisons between treatments were made one at a time (e.g., Exclosure Year 1 - 2012 vs. Active Prairie Dogs - 2012) and grouped by site ID. When examining temporal effects, we used sampling year as the fixed effect to quantify differences in
the same treatment (e.g., Uncolonized - 2012 vs. Uncolonized - 2013). In order to determine the different species or cover classes that were driving the compositions of each treatment, we ran a Dufrene-Legendre indicator species analysis with the indval function from the labdsv package in R (Roberts 2012). Unlike running multiple correlations between different species and the NMDS axes, the indicator species analysis is not confounded by potential correlations between different species, and therefore was a superior choice for quantifying the effects of different species on treatment compositions.

In order to examine treatment differences in the relative cover of different vegetation groups (i.e. bare soil, litter, native forbs, introduced forbs, native grasses, and introduced grasses) and Shannon-Weiner diversity values, analyses were conducted with linear mixed models (LMMs) utilizing the lme4 package (Bates et al. 2012) in R in order to account for the correlation caused by the exclosure sampling design. Unlike the PERMANOVA analysis, the LMMs allow the inclusion of multiple random effects into the model; therefore we were able to use all of our sampling data. The models that we used to determine the effect of the different treatments on the relative cover of specific vegetation groups included a fixed effect of treatment (e.g., Active Prairie Dogs or Exclosure Year 3) and the random effects of sample year (2012-2014), sample month (June through August), and colony ID number. Including the random effects of sample year, sample month, and colony ID accounted for the repeated measures inherent in the sampling design.

Results

Vegetation Community Compositions

There was no significant difference in plant community composition between the active prairie dog communities and the colonized transects for any time in the study period ($P > 0.05$
for all). The communities representing each individual exclosure plot treatment for each year (i.e. Active Prairie Dogs - 2012, Active Prairie Dogs - 2013, Active Prairie Dogs - 2014, Exclosure Yr. 1 - 2012, Exclosure Yr. 1 - 2013, Exclosure Yr. 2 - 2013, Exclosure Yr. 2 - 2014, and Exclosure Yr. 3 – 2014) were all significantly different from each other (P < 0.001 for all; Fig. 3-1), and were all significantly different from the uncolonized transect communities (Uncolonized - 2012, Uncolonized - 2013, and Uncolonized - 2014; P < 0.001 for all). The uncolonized plots from 2012 and 2013 were the only two communities that were not significantly dissimilar (P = 0.72).

![Figure 3-1](image_url)

**Fig. 3-1.** Changes in exclosure community compositions established in 2012 (dark grey) and 2013 (light grey) over time relative to the uncolonized transect communities (open triangles) and active prairie dog areas (open circles). Arrows indicate the annual change directional path for the different treatments. Each symbol represents the average NMDS score for each treatment each year. Error bars omitted for clarity. Stress = 0.20 with all treatments.

Bare soil was the cover class with the highest indicator value for the active prairie dog areas, but was not one of the top five highest indicators in the exclosure year 2, exclosure year 3, or uncolonized communities (Table 3-2). Similarly, the exotic forb *Convolvulus arvensis*, had a top five indicator value for the active prairie dog areas, exclosure year 1, and exclosure year 2,
but was not in the top five for either of the exclosure year 3 or uncolonized communities. Unlike
the active prairie dog areas and the exclosure communities, the five species with the highest
indicator values for the uncolonized areas were all grasses.

Table 3-2. The five cover classes with the highest species indicator values for each
treatment. All plant species identified with origin (native (N) or introduced (I)) and
lifeform (forb or grass).

<p>| Active prairie dog colonies                     |</p>
<table>
<thead>
<tr>
<th>Indicator value</th>
<th>Species or Cover Name</th>
<th>Origin</th>
<th>Lifeform</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.58</td>
<td>Bare Soil</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>0.22</td>
<td>Convolvulus arvensis</td>
<td>I</td>
<td>Forb</td>
</tr>
<tr>
<td>0.16</td>
<td>Litter</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>0.07</td>
<td>Verbena bracteata</td>
<td>N</td>
<td>Forb</td>
</tr>
<tr>
<td>0.05</td>
<td>Chamaesyce serpyllifolia</td>
<td>N</td>
<td>Forb</td>
</tr>
</tbody>
</table>

<p>| Exclosure year 1                           |</p>
<table>
<thead>
<tr>
<th>Indicator value</th>
<th>Species or Cover Name</th>
<th>Origin</th>
<th>Lifeform</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.38</td>
<td>Chenopodium desiccatum</td>
<td>N</td>
<td>Forb</td>
</tr>
<tr>
<td>0.33</td>
<td>Convolvulus arvensis</td>
<td>I</td>
<td>Forb</td>
</tr>
<tr>
<td>0.23</td>
<td>Bare Soil</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>0.15</td>
<td>Litter</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>0.11</td>
<td>Pascopyrum smithii</td>
<td>N</td>
<td>Grass</td>
</tr>
</tbody>
</table>

<p>| Exclosure year 2                           |</p>
<table>
<thead>
<tr>
<th>Indicator value</th>
<th>Species or Cover Name</th>
<th>Origin</th>
<th>Lifeform</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>Litter</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>0.21</td>
<td>Convolvulus arvensis</td>
<td>I</td>
<td>Forb</td>
</tr>
<tr>
<td>0.14</td>
<td>Chenopodium desiccatum</td>
<td>N</td>
<td>Forb</td>
</tr>
<tr>
<td>0.12</td>
<td>Taraxacum officinale</td>
<td>I</td>
<td>Forb</td>
</tr>
<tr>
<td>0.11</td>
<td>Pascopyrum smithii</td>
<td>N</td>
<td>Grass</td>
</tr>
</tbody>
</table>

<p>| Exclosure year 3                           |</p>
<table>
<thead>
<tr>
<th>Indicator value</th>
<th>Species or Cover Name</th>
<th>Origin</th>
<th>Lifeform</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.46</td>
<td>Lactuca serriola</td>
<td>I</td>
<td>Forb</td>
</tr>
<tr>
<td>0.40</td>
<td>Tragopogon dubius</td>
<td>I</td>
<td>Forb</td>
</tr>
<tr>
<td>0.27</td>
<td>Lithospermum incisum</td>
<td>N</td>
<td>Forb</td>
</tr>
<tr>
<td>0.24</td>
<td>Artemisia frigida</td>
<td>N</td>
<td>Forb</td>
</tr>
<tr>
<td>0.22</td>
<td>Pascopyrum smithii</td>
<td>N</td>
<td>Grass</td>
</tr>
</tbody>
</table>

<p>| Uncolonized                     |</p>
<table>
<thead>
<tr>
<th>Indicator value</th>
<th>Species or Cover Name</th>
<th>Origin</th>
<th>Lifeform</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.51</td>
<td>Andropogon gerardii</td>
<td>N</td>
<td>Grass</td>
</tr>
<tr>
<td>0.47</td>
<td>Chondrosum gracile</td>
<td>N</td>
<td>Grass</td>
</tr>
<tr>
<td>0.44</td>
<td>Bouteloua curtipendula</td>
<td>N</td>
<td>Grass</td>
</tr>
<tr>
<td>0.38</td>
<td>Poa compressa</td>
<td>I</td>
<td>Grass</td>
</tr>
<tr>
<td>0.35</td>
<td>Bromus japonicus</td>
<td>I</td>
<td>Grass</td>
</tr>
</tbody>
</table>
Comparison of Vegetation Communities

The exclosure plot treatments had significant effects on the relative covers of bare soil, introduced forbs, native forbs, native grasses, introduced grasses, and litter (Table 3-3). The relative cover of bare soil in the active prairie dog plots was significantly greater than the relative cover of bare soil in all of the prairie dog exclosure communities as well as the uncolonized transects ($P < 0.001$ for all; Fig. 3-2A). In one year of prairie dog exclusion, the relative cover of bare soil declined from an average of 26.7% to 16.4% in the exclosure year 1 plots, and bare soil only constituted 1.1% of the relative cover by exclosure year 3.

Table 3-3. Average relative cover of different cover class groups for the different experimental treatments. Means ± standard error presented.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bare Soil</th>
<th>Introduced Forbs</th>
<th>Native Forbs</th>
<th>Introduced Grasses</th>
<th>Native Grasses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active prairie dog colonies</td>
<td>0.267 ± 0.02</td>
<td>0.413 ± 0.02</td>
<td>0.082 ± 0.01</td>
<td>0.001 ± 0.00</td>
<td>0.033 ± 0.01</td>
</tr>
<tr>
<td>Exclosure Yr. 1</td>
<td>0.164 ± 0.01</td>
<td>0.459 ± 0.03</td>
<td>0.117 ± 0.01</td>
<td>0.001 ± 0.00</td>
<td>0.089 ± 0.02</td>
</tr>
<tr>
<td>Exclosure Yr. 2</td>
<td>0.037 ± 0.01</td>
<td>0.398 ± 0.02</td>
<td>0.132 ± 0.01</td>
<td>0.002 ± 0.01</td>
<td>0.103 ± 0.01</td>
</tr>
<tr>
<td>Exclosure Yr. 3</td>
<td>0.011 ± 0.01</td>
<td>0.425 ± 0.03</td>
<td>0.108 ± 0.02</td>
<td>0.001 ± 0.00</td>
<td>0.144 ± 0.02</td>
</tr>
<tr>
<td>Uncolonized</td>
<td>0.069 ± 0.01</td>
<td>0.033 ± 0.01</td>
<td>0.064 ± 0.01</td>
<td>0.132 ± 0.02</td>
<td>0.233 ± 0.02</td>
</tr>
</tbody>
</table>

The relative cover of introduced forbs in the active prairie dog plots was significantly greater than all other treatments ($P < 0.05$ for all; Fig. 3-2B); however there was no significant difference in the relative cover of introduced forbs between the different exclosure plot years ($P > 0.05$ for all). The relative cover of introduced forbs in the uncolonized transects (3.3%), was 12.5 times less than the relative cover in the exclosure year 3 plots (42.6%) and significantly lower than all treatments ($P < 0.001$ for all). The relative cover of both native forbs and native grasses increased in the prairie dog exclosures. With an average relative cover of 8.2% in the
active prairie dog plots, the relative cover of native forbs increased significantly in exclosure year 1 (11.7%) and exclosure year 2 (13.2%; \( P < 0.05 \) for both; Fig. 3-2C), before declining to 10.8% in exclosure year 3, a level not significantly different from the relative cover of native forbs documented on the uncolonized transects \( (P = 0.2) \). Similarly, the relative cover of native grasses significantly increased from 3.3% in the active prairie dog plots to 8.9% in the exclosure year 1 plots and 14.4% by exclosure year 3 \( (P < 0.05 \) for all; Fig. 3-2D), however, the relative cover of native grasses in the exclosure year 3 plots was still significantly lower than the 23.3% average relative cover documented in the uncolonized transects \( (P < 0.001) \).

Introduced grasses had almost no growth in the exclosure plots. In the active prairie dog plots, introduced grasses constituted 0.1% of the relative cover, which was the same amount observed in exclosure years 1 and 3; exclosure year 2 had a 0.2% relative cover of introduced grasses. There were no significant differences in the relative cover of introduced grasses between the different exclosure treatments or the active prairie dog plots \( (P > 0.05 \) for all). However, introduced grasses constituted 13.1% of the relative cover in the uncolonized transects, which was significantly greater than the active prairie dog plots as well as all of the exclosure treatments \( (P < 0.001 \) for all).

**Community Metrics**

The Shannon-Weiner species diversity of the active prairie dog plots was significantly lower than the values from all of the exclosure treatments \( (P < 0.05 \) for all; Fig. 3-3A). The mean diversity values of the exclosure year 1 plots (0.65) were significantly lower than the values in exclosure year 2 (1.09) and exclosure year 3 (1.32; \( P < 0.05 \) for all). The diversity of the uncolonized transects was significantly greater than the values of the exclosure communities \( (P > 0.05 \) for all), and 40% higher than the value of exclosure year 3.
Fig. 3-2. Boxplots demonstrating the average relative cover of bare soil (A), introduced forbs (B), native forbs (C), and native grasses (D) for the exclosure treatments and uncolonized areas. The bold horizontal lines indicate the median value, while the ends of the box correspond to the upper and lower quartiles. Different letters indicated significant differences between treatments at the $P < 0.05$ level.
The introduced species diversity increased significantly from the active prairie dog plots (0.07) to exclosure year 2 (0.52; \( P < 0.05 \) for all; Fig. 3-3B). Furthermore, the introduced species diversity in the uncolonized transects was significantly higher than the amount in the exclosure year 3 plots (\( P = 0.01 \)). Native species diversity increased significantly from the active prairie dog plots to exclosure year 1 (\( P < 0.001 \); Fig. 3-3C), but was not different among the exclosure year treatments (\( P > 0.05 \) for all). With a mean value of 1.74, the native species diversity of the uncolonized transects was 2.5 times greater than the native diversity in exclosure year 3 (0.69), and significantly greater than all exclosure treatments (\( P < 0.05 \) for all).

**Fig. 3-3.** Boxplots demonstrating all species diversity (A), introduced species diversity (B), and native species diversity (C) for the exclosure treatments and uncolonized areas. The bold horizontal lines indicate the median value, while the ends of the box correspond to the upper and lower quartiles. Different letters indicated significant differences between treatments at the \( P < 0.05 \) level.
**Discussion**

Our study used three main approaches to examine if removing prairie dogs for three years from novel communities at the urban-wildland interface resulted in changes compatible with the notion that plant communities would return to compositions equivalent to nearby uncolonized areas. Due to successful short term restorations in more natural prairie systems (Hartley et al. 2009, Augustine et al. 2014), prairie dog removal is considered an intervention option in heavily anthropogenically-influenced landscapes. However, the novel plant compositions on prairie dog colonies at the urban-wildland interface contain new abiotic and biotic conditions which will directly affect the restoration outcome. Since the timing of a restoration effort can be heavily influenced by annual climatic factors, such as temperature and precipitation, our analysis also examined temporal effects on restoration.

Our analysis indicated that the OSMP colonized vegetation transects and our active prairie dog communities were not different with respect to community composition for each year during the study period. This finding suggests that although the exclosure plots and OSMP transects utilized different sampling methods to quantify plant community compositions, the sampling approaches resulted in similar compositions. Based on this finding, we believe that including the uncolonized OSMP transects in the exclosure plot analysis is justifiable, and provides a valuable benchmark to measure the restoration trajectory of the exclosure plots.

In more natural landscapes, prairie dog removal for 3-5 years allowed grasses to reestablish and returned plant communities to compositions equivalent to uncolonized areas (Hartley et al. 2009; Augustine et al. 2014), leading some land managers at the urban-wildland interface to propose prairie dog removal as an intervention method to reduce introduced plants and restore native vegetation communities (e.g. Boulder County Parks and Open Space 2012).
However, the findings of this study have shown that three years of prairie dog removal in a heavily anthropogenically-influenced landscape did not have the same effect as previously documented. The trajectory of change for the exclosure communities was generally towards the uncolonized areas, however, the results of the indicator species analysis suggests that these changes were driven by plant regrowth rather than changes in plant community composition. This was best illustrated by the indicator species analysis results which showed bare soil as the top cover class driving the composition of the active prairie dog areas, but the importance of bare soil declined to the third most important cover class in exclosure year 1 and fell out of the top five driving compositions by exclosure year 2. Additionally, our analyses showed at the end of the study period in 2014, the exclosure community compositions (i.e., Exclosure Yr. 2 - 2014 and Exclosure Yr. 3 - 2014) were on a trajectory of change away from both the active prairie dog areas and the uncolonized communities. The differences between the exclosure year 3 and uncolonized communities were further illustrated by examining the species responsible for driving the compositions, which showed that the top four species in the exclosure year 3 compositions were forbs and the top five species in the uncolonized compositions were all grasses. The compositional changes observed in the older exclosure communities could demonstrate the suggestion of Suding et al. (2004) that management failure to address all of the constraints when restoring an ecosystem can have the unintended consequences of shifting the system to a new alternative state, on a trajectory unaligned with the restoration goal. While it is uncertain if the exclosure communities represent alternative states, it is clear that the oldest exclosure communities contain new compositions that are dissimilar from both the active prairie dog areas and the uncolonized areas. Examining the restoration trajectory of the exclosure...
communities suggests that three years of prairie dog removal at the urban-wildland interface did not restore plant communities to compositions equivalent to uncolonized areas.

By establishing exclosures in two different years, our study design allowed us to observe potential temporal effects on the restoration outcome. Temporal effects on restoration could arise from annual climate variability, or high-impact events such as droughts, which could dramatically effect plant growth. The 2012 growing season had the highest mean temperature during the study period, while the 2013 growing season had the lowest amount of precipitation. The trajectory of change for the exclosure communities established in 2012 and 2013, as well as the active prairie dog areas and the uncolonized communities, clearly shows that there is annual variability in all community compositions, which is not surprising given the annual variations in local climatic factors. However, from 2012-2014 we observed less variability in the uncolonized communities than the active prairie dog communities. While the observation period was only three years, these findings provide additional support to the idea that presence of prairie dogs in heavily anthropogenically-influenced landscapes amplifies low-intensity directional changes, such as non-native species introduction and climate change, compared to uncolonized areas (Beals et al. 2014). In addition, the pattern of change shown by the two exclosure communities over time is similar to the trajectory of the active prairie dog areas, except that the annual changes in the active prairie dog areas is less pronounced. Despite the one year difference in prairie dog removal time, the restoration trajectory of the exclosure communities established in 2012 and 2013 nearly converges in 2014. In fact, the Exclosure Yr. 2 - 2014 community is more similar to the Exclosure Yr. 3 - 2014 community than it is to the Exclosure Yr. 2 – 2013 community which has excluded prairie dog grazing for the same amount of time. These findings regarding the temporal effects further support the well-established link between precipitation and
restoration (e.g., Bai et al. 2004), but also suggest that potential differences in restored communities may diminish with time.

Prairie dog removal had an immediate impact on the relative cover of each vegetation group that we examined, and the differences between the active prairie dog and exclosures areas grew as prairie dog removal time increased. As was also evident from the indicator species analysis, bare soil declined dramatically after only one year of prairie dog removal but examination of vegetation groups shows that forbs, predominantly those introduced in origin, and not grasses, were the species reestablishing in the absence of prairie dog grazing. The exclosure year 3 plots were on average 14.5% grasses and 53.3% forbs compared to the uncolonized areas that were on average 36.5% grasses and 9.7% forbs. This higher prevalence of forbs may reflect changes to the biogeochemical functioning of these grassland ecosystems (e.g., Vitousek et al. 1987, Ehrenfeld 2010), and could produce additional abiotic disparities between the colonized and uncolonized areas. Aside from the grass to forb ratio, neither the exclosure year 3 compositions, nor any of the other exclosure communities, contained a relative cover of native grasses or introduced forbs that resembled the covers observed in the uncolonized areas. Native forbs were the only vegetation group with similar covers in the exclosures and in the uncolonized areas, but with relative cover values averaging less than 15%, native forbs are not the dominant species in uncolonized grassland communities. Therefore, due to the differences in relative cover of native grasses, introduced forbs, and the grass to forb ratio, it is evident that three years of prairie dog removal in a heavily anthropogenically-influenced landscape did not return vegetation groups to levels equivalent to those observed in uncolonized areas.
Although introduced forbs dominated the exclosure plots, the lack of introduced grass species growth within the exclosure plots was unexpected. In the Western US, introduced grasses have received extensive attention from rangeland managers and researchers due to their successful proliferations and subsequent ecosystem effects (e.g., D’Antonio and Vitousek 1992, Whisenant 1990). In this study, introduced grasses constituted 13.1% of the relative cover in the uncolonized transects but only 0.1% of the relative cover in the exclosure year 3 communities. However, the relative cover of native grasses increased more than four times from the active prairie dog plots to exclosure year 3, indicating that grass recovery is possible and success could be related to phenology. Some introduced grasses, such as *Bromus tectorum*, are successful invaders by utilizing available soil water to grow earlier in the spring than native species (Melgoza et al. 1990). While this may be a successful strategy in most grassland areas, prairie dog colonies in a heavily anthropogenically-influenced landscape contain higher levels of bare soil exposure, and less litter than uncolonized areas (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015). Therefore, by germinating in autumn or the early spring and growing before other species on densely populated prairie dog colonies at the urban-wildland interface, introduced grasses may be exposed to extremely high levels of herbivory, severely limiting their ability to survive until reproduction and ultimately minimizing their presence in the seed bank. During non-growing season months, we have regularly observed prairie dogs digging for seedlings, which has created extensive pitting across numerous colonies (Fig. 3-4). Although this study did not examine the presence of introduced grass species in the seed bank on prairie dog colonies, or seed dispersal processes, it is clear that introduced grasses, which are typically successful in adjacent grassland areas without prairie dogs, were unsuccessful at proliferating in the prairie dog exclosures. This suggests that prairie dog grazing in a heavily anthropogenically-
influenced landscape may control introduced grasses on colonies, a novel effect not previously associated with prairie dogs.

![Image](image.jpg)

**Fig. 3-4.** Pitted surface of a prairie dog colony at the urban-wildland interface created by prairie dogs digging for plant seedlings outside of the growing season. Photo taken on March 23, 2015 in Broomfield, Colorado, USA.

Plant community diversity was greatly affected by prairie dog removal. The diversity of all plants increased in exclosure year 1 and again in exclosure year 2, however, the increased diversity was driven primarily by an increase in introduced plant diversity, not native plants. In fact, native plant diversity did not change with exclosure plot age, and was less than half of the native diversity in the uncolonized areas. Examination of vegetation groups as well as the diversity of the exclosure treatments has shown that native vegetation is slow to reestablish in the
exclosures plots, and that the majority of vegetation growing within the exclosures are introduced forbs. The lack of native plant reestablishment in the exclosures may be directly related to landscape context.

One major difference between urban-wildland areas and more natural landscapes involves the extent of native vegetation adjacent to colonies, which can be abundant in natural areas but typically exist only as fragments in a heavily anthropogenically-influenced landscape. Native seed source availability is crucial in restoring historically common plant communities (Suding et al. 2004), but the urban-wildland interface contains fewer sources of native seeds as well as anthropogenic features that may inhibit seed dispersal. Therefore it should not be surprising that prairie dog colony plant communities at the urban-wildland interface do not recover in the same manner or timeline observed in more natural areas. It is possible that long term prairie dog removal, for periods of 10 or more years, could allow for the gradual reestablishment of native species and a return of communities that are equivalent to the uncolonized areas, however, it is clear that three years of prairie dog removal did not reestablish communities with plant diversity levels that were equivalent to those found in uncolonized areas.

Conclusions

Grassland habitat is being lost and degraded in the Western U.S. faster than it is being protected (Hoekstra et al. 2005). Without preserving and restoring the remaining habitat, the ecological services and function that these areas once provided could be lost. Prairie dogs historically played a valuable ecological role, and their presence is assumed to assist grassland restoration efforts. However, recent research has shown that the ecological role of prairie dogs has changed in heavily anthropogenically-influenced landscapes, and that their presence had produced novel plant communities on colonies. As human development in the Western U.S.
continues, interactions at the urban-wildland interface will increase, and the need to restore the novel plant communities on prairie dog colonies will become more urgent. However, the new abiotic and biotic conditions on prairie dog colonies present major restoration challenges. This study examined the effect of prairie dog removal on plant community compositions, vegetation groups, and plant diversity and it is clear that three years of prairie dog removal did not restore plant communities to the levels equivalent to those found on areas without prairie dogs. Although prairie dog removal restored plant communities in more natural areas, the biotic conditions on colonies at the urban-wildland interface, such as plant community compositions and native seed source availability, are likely responsible for making three years of prairie dog removal an ineffective intervention effort in a heavily anthropogenically-influenced landscape. Similar restoration efforts conducted over longer time periods may be more successful and should be explored in the future. This study demonstrates that passive restoration of novel plant communities is potentially problematic due to multiple, non-historically present and potentially directional changes and provides a valuable example to our understanding of novel ecosystem restoration, as well as emphasizing the role and effect of landscape context on ecosystems and restoration.
CHAPTER 4
FROM KEYSTONE SPECIES TO ECOSYSTEM ENGINEER: THE CHANGED ROLE OF A NATIVE CONSUMER AT THE URBAN-WILDLAND INTERFACE


Abstract
As a native keystone species, prairie dogs in more natural prairie landscapes regulate important ecosystem services, and therefore play a critical role for long-term suitability. However, recent research at the urban-wildland interface has shown that prairie dogs elicit unexpected plant community changes, which may result in different ecosystem services than have been historically provided. We examined the soil stability, plant aboveground net primary productivity (ANPP), and soil fertility of prairie dog colonies and adjacent uncolonized areas to test if these three ecosystem services, regulated by prairie dogs in natural landscapes, are maintained at the urban-wildland interface. Monthly aeolian sediment flux monitoring revealed nearly ten times more material emanating from prairie dog colonies compared to uncolonized grassland areas, demonstrating that erosion rates are enhanced by prairie dogs at the urban-wildland interface. Furthermore, the percent of total carbon and nitrogen in surface soils collected from prairie dog colonies were less than the amounts observed in adjacent uncolonized areas, suggesting lower soil fertility on colonies. Although prairie dog colony ANPP did not decline with increasing colony age, analysis of plant groups revealed that introduced forb ANPP increased with colony age, while the ANPP of native forbs, native grasses, and introduced grasses all declined. This research demonstrates that multiple ecosystem service benefits associated with the presence of prairie dogs in more natural landscapes are not maintained at the urban-wildland interface. In addition to emphasizing the effect that landscape context and human
development can have on a native species’ ecological role, these findings provide critical information for future sustainable management decisions.

**Introduction**

Native keystone species conservation is generally considered essential in regulating historical ecosystem function, structure, and services (Estes and Palmisano 1974, Smith et al. 2003). In degraded and vulnerable ecosystems, the value of a native keystone species typically increases due to their critical regulating role. With continuous development in the Western U.S., grassland ecosystems are being lost or degraded due to anthropogenic impacts at rates exceeding their protection (Hoekstra et al. 2005). Based on conventional knowledge, the conservation of black-tailed prairie dogs (*Cynomys ludovicianus*; henceforth prairie dogs), a native keystone species once abundant in Western U.S. grasslands (Merriman 1902, Kotliar et al. 1999), appears as a logical management effort to preserve historical grassland ecosystem structure, function, and services. However, in complex modern grasslands with overwhelming anthropogenic effects, the functional role of prairie dogs has been altered (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015), with unknown ecosystem level changes. Examining the effects of prairie dogs on ecosystem services at the urban-wildland interface will provide insight into the regulating role of a native keystone species operating outside of its historical state as well as directly informing future grassland management decisions.

The vast majority of research on prairie dogs, which has developed current public opinion and management decisions, has been conducted in low anthropogenically-influenced landscapes, such as Wind-Cave National Park (e.g., Archer and Detling 1987, Detling 1998) and the Pawnee National Grassland in Colorado (e.g., Whicker and Detling 1988). This research has connected the presence of prairie dogs to numerous ecosystem benefits including providing habitat for
macro-invertebrates (Miller et al. 1994), as well as increasing plant community diversity and richness (Bonham and Lerwick 1976, Coppock et al. 1983). More recently, researchers in the Janos Biosphere Reserve in Chihuahua, Mexico, observed prairie dogs regulating multiple ecosystem services including soil stability and forage biomass (Martínez-Estévez et al. 2013). While the valuable ecological role that prairie dogs play in natural prairie systems is indisputable, recent studies conducted at the urban-wildland interface have revealed unexpected plant community changes on prairie dog colonies, such as the loss of native grasses and proliferation of introduced forbs, which are most likely the result of multiple anthropogenic drivers of change (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015). Prairie dog colony densities increase at the urban-wildland interface, potentially due to a lack of predator access and inability of prairie dogs to disperse across anthropogenic features (Johnson and Collinge 2004), which may subsequently result in large exposed areas of bare soil and reduced plant cover compared to colonies in more natural prairie landscapes (e.g., Beals et al. 2014, Hopson et al. 2015). In more natural systems, these bare soil voids typically undergo native forb recruitment (e.g., Bonham and Lerwick 1976), but in heavily anthropogenically-influenced landscapes, these voids are exploited by non-native forbs already present in the region (Beals et al. 2014). Some prairie dog colonies at the urban-wildland interface contain plant communities so disparate from historically common communities that they have been deemed novel since no natural analog exists (Beals et al. 2014).

Due to the link between plant community composition, ecosystem structure, and ecosystem function (e.g., Vitousek et al. 1987, Mack et al. 2001, Ehrenfeld 2003), the plant community shifts on colonies at the urban-wildland interface suggests the potential for prairie dogs to additionally alter ecosystem level processes, and ultimately impact the long-term
sustainability of these valuable areas. However, the regulating role of prairie dogs at the urban-wildland interface has not been examined, forcing managers to make decisions without proper information. As human development in the Western U.S. continues, prairie dogs inhabiting grasslands at the urban-wildland interface will become the norm rather than the exception. Therefore, understanding the constrained functional role of prairie dogs imposed by anthropogenic impacts will become critical for future management as well as contribute to our understanding regarding native keystone species operating outside of their historical states.

Here we present a study that examines soil erosion regulation, aboveground plant productivity, and soil fertility, three ecosystem services provided by prairie dog colonies in a heavily anthropogenically-influenced landscape. Eradication campaigns on private properties in the Western U.S. since the early 1900s has restricted many prairie dog populations to public lands. These same public lands must now support and provide numerous ecosystem services, including wild life viewing, walking trails, and livestock grazing. Although the presence of prairie dogs undoubtedly provides a beneficial service to most conservationists and wildlife viewers, there may be long-term effects on the grassland ecosystems that may reduce other critical ecosystem services, such as erosion control, plant productivity, and soil fertility. Without understanding the ecosystem level changes resulting from the presence of prairie dogs at the urban-wildland interface, successful long-term sustainable management of grassland areas with prairie dogs is unlikely.

Erosion regulation is an essential ecosystem service provided by countless flora and fauna across the globe. Wind erosion is considered to be one of the greatest contributors to declining soil fertility in some prairie ecosystems due to the loss or redistribution of nutrient-rich topsoil (Larney et al. 1994, Larney et al. 1998), and high erosion events, such as dust storms, can
cause human health and safety hazards (Griffin et al. 2001). In a less anthropogenically-influenced landscape, prairie dog colonies were documented with a level of soil stability equal to those found in uncolonized grassland areas (Martínez-Estévez et al. 2013), however, changes to plant communities and the vegetation loss observed on prairie dog colonies at the urban-wildland interface (Beals et al. 2014) suggests that this regulating role may have changed for prairie dogs. Due to high population densities, prairie dog colonies at the urban-wildland interface have been documented with a cover of bare soil nearly four times greater than the amount found on adjacent uncolonized areas (Beals et al. 2014) and more than 40% higher than the bare soil cover observed on prairie dog colonies in more natural prairie landscapes (e.g., Archer et al. 1987). Low plant cover and large expanses of bare soil are highly vulnerable to wind erosion (Breshears et al. 2009, Munson et al. 2011), suggesting that prairie dog colonies at the urban-wildland interface have the potential to be more erosive compared to adjacent uncolonized areas. High rates of wind erosion, or aeolian sediment flux, originating from prairie dog colonies could produce human health and safety hazards, as well as alter the soil fertility on colonies over time. Examining aeolian sediment flux rates on prairie dog colonies at the urban-wildland interface will provide insight into the effect of prairie dog colonization on wind erosion, one ecosystem service regulated by the presence of prairie dogs in more natural landscapes.

The relationship between the presence of prairie dogs, aboveground plant productivity, and forage biomass has been a contentious topic between ranchers and conservationists for decades due to the large scale economic impacts resulting from this valuable ecosystem service (e.g., Miller et al. 1994, Vermeire et al. 2004). In 1902, Merriman’s observation that prairie dogs reduced grazing forage, and therefore decreased livestock carrying capacity, was a primary factor used to justify extensive eradication campaigns (Merriman 1902). In the past two decades, a
contentious debate over the ability of prairie dogs to reduce the carrying capacity of colonized areas for large herbivores and livestock has reemerged without a definitive conclusion (see Miller et al. 1994, Vermeire et al. 2004, and Miller et al. 2007). While these findings contribute to our general understanding regarding the regulating role of prairie dogs on forage biomass, the entirety of this research has been conducted in natural prairie landscapes which contain dramatically different abiotic conditions and biotic communities compared to prairie dog colonies at the urban-wildland interface. Furthermore, the elevated prairie dog densities and potentially increased aeolian sediment flux rates on colonies are two drivers of change encountered at the urban-wildland interface that may synergistically impact forage biomass and aboveground productivity, by reducing soil carbon, nitrogen, and other nutrients essential for plant growth over time (de Jong and Kachanoski 1988, Yan et al 2013). As colonies become older, continued depletion of soil carbon and nitrogen through grazing and increased wind erosion may result in decreased soil fertility as a function of colony age; however the relationships between colony age, plant productivity, and soil fertility have not been examined in a complex modern landscape.

Due to the increased cover of base soil and plant compositional shifts observed on prairie dog colonies at the urban-wildland interface, there is reason to believe that some ecosystem services regulated by the presence of prairie dogs in natural landscapes are not maintained in a heavily anthropogenically-influenced landscape. We attempted to test this here by examining soil and plant characteristics of prairie dog colonies at the urban-wildland interface. We quantified surface soil carbon (C) and nitrogen (N) content from both uncolonized areas and active prairie dog colonies that varied in colonization duration. We also measured aeolian sediment emission rates on and off prairie dog colonies, and examined the C and N content of the wind eroded
material. In order to investigate prairie dog colony plant characteristics at the urban-wildland interface, we concurrently quantified the relationship between prairie dog colony age and plant aboveground net primary productivity (ANPP). We believe that the findings of this study will contribute to our understanding of the ecosystem level changes resulting from the presence of prairie dogs at the urban-wildland interface and can be used to inform future long-term sustainable management decision.

**Methods**

**Study Area**

All data were collected east of the Foothills of the Rocky Mountains, within Boulder and Broomfield Counties, in Colorado, USA. This study centers on public lands managed by the City of Boulder Open Space and Mountain Parks (OSMP) and Broomfield Open Space. Prior to extensive human development, prairie dogs in this region established colonies within the short and mixed-grass ecosystems that were historically common in the area. Continued development in the region since the 1940s has produced a complex matrix of anthropogenic features, principally roads and buildings, which surround the public lands harboring prairie dog colonies (Johnson and Collinge 2004, Beals et al. 2014). Prairie dog colony boundaries have been mapped annually by OSMP personnel since 1997. In 2014, prairie dogs occupied approximately 1235.07 ha on OSMP properties. We used ArcGIS 10.2 (ESRI, Redlands, CA, USA) to determine the age of each colony and verified these data with OSMP field notes and personal conversations with land managers. All prairie dog colonies examined by this work were located between 40°6’17” and 39°53’32” N and 105°16’50” and 105°5’15” W with an approximate mean elevation of 1645 m. Soils in the study area are generally a combination of Aridisols, the primary grassland soil, and Mollisols, which are rich in organic matter (Moreland and Moreland 1975). Parent material
is variable, but most soils are derived from eroded alluvium and colluvium deposited from Pliocene to Pleistocene outwash events and from subsequent erosion of materials from the foothills of the adjacent Rocky Mountains. The NOAA Earth Systems Research Lab in Boulder, Colorado, recorded April-August total precipitation values of 22.40 cm in 2012, 24.99 cm in 2013, and 33.81 cm in 2014 (www.esrl.noaa.gov/psd/boulder).

Aeolian Sediment Flux

The amount of aeolian sediment flux on prairie dog colonies and nearby uncolonized areas was quantified with “Big Spring Number Eight” (BSNE) sediment collectors. The BSNE is a passive aeolian-aspirated sediment sampler affixed to a pole and weather vane that self-orient into the wind (Fryrear 1986). Sixteen BSNE samplers were set at 15 cm above the ground in an on/off colony paired design on seven different prairie dog colonies in the study area. Six of the seven prairie dog colonies with BSNE samplers were older than 12 years in 2014 and greater than 10 ha in area. None of the prairie dog colonies with BSNE samplers had a known history of agricultural tilling or grazing by livestock. The samplers located on prairie dog colonies were established in the approximate colony center, since these areas have typically been occupied the longest, while the off colony samplers were positioned within 300 m of the on colony sampler and greater than 50 m from the colony edge. No BSNE sampler was positioned in a location that would artificially influence sediment flux rates, such as in lee of an object. Vegetation directly below the samplers was periodically clipped if it limited sampler movement.

From July 2014 - June 2015 all BSNE samplers were cleaned on the first week of each month, with the exception of February and March 2015 when cleaning was delayed for up to three days due to inaccessibility caused by inclement weather. The sediment collected by each
sampler was dried at 60° C in a forced-air oven for a minimum of 72 hours then air-equilibrated prior to weighing. Sediment flux was calculated by dividing the monthly sample mass by the BSNE sampler opening area (10 cm²) and the number of days within the sampling period (Flagg et al. 2014), and therefore, is reported as grams/meter²/day (g m⁻² d⁻¹).

Prior to establishing the paired BSNE sampler design in June 2014, we set six BNSE samplers on four prairie dog colonies from March 2013 to March 2014 to examine the soil characteristics and potential fertility of the wind eroded material. Similar to the paired study, the BSNE samplers were set to 15 cm above the soil surface, and all of the colonies used to measure the potential fertility of the eroded material in 2013 were used to quantify sediment flux in 2014. The material collected by each BSNE sampler was composited into a single sample that represented the entire sample year then processed with a 2 mm sieve. The samples were dried in a forced-air oven at 41° C for a minimum of 72 hours, then prepped and analyzed by a ThermoQuest ® Flash EA 1112 model CHN analyzer to quantify the percentage of both total carbon (TC) and total nitrogen (TN), which were used as proxy fertility estimates.

**Soil Characteristics and Colony Age**

Total carbon and TN were used as a proxy estimate of surface soil fertility from prairie dog colonies and adjacent uncolonized areas at the urban-wildland interface. We collected soil cores at depths of 0-10 cm from 11 prairie dog colonies varying in colonization duration and adjacent off colony areas in Boulder and Broomfield counties. Similar to the aeolian sediment flux monitoring, soil core sampling was conducted in an on/off colony paired design, although one off colony sample could not be collected due to the presence of roads entirely surrounding
the colony extent. Soil cores were collected from all of the colonies used for the ANPP measurements in addition to six other prairie dog colonies in Boulder County.

At each of the 11 colony sampling locations, three replicates of ten soil samples were randomly collected from the prairie dog colony center and an adjacent uncolonized area. The soil samples were taken from depths of 0-10 cm, since this depth historically included only ‘A’ horizon materials (Moreland and Moreland 1975) and represents the location where the majority of net nitrogen mineralization occurs (Frank and Groffman 1998). The replicates were composited into a single sample, processed with a 2 mm sieve, and dried at room temperature for multiple days. From each on/off colony sample, a 5 g subsample was taken, ground with a ball mill, and then dried in a forced-air oven at 41°C for a minimum of 72 hours. Following preparation, all soil samples were analyzed with a ThermoQuest ® Flash EA 1112 model CHN analyzer to determine the percentage of TC and TN.

**ANPP and Colony Age**

To quantify aboveground ANPP on prairie dog colonies, we used the moveable exclosure method (McNaughton 1979) to best estimate herbivore consumption and plant regrowth responses (McNaughton et al. 1996, Fahey and Knapp 2007). On each of five colonies, a series of ten temporary 0.25 m² exclosures were set beginning in March 2012. All prairie dog exclosures were established in the active areas of colonies, more than 50 m from the colony edge. When the study began in 2012, one prairie dog colony has been occupied for four years, one for eight years, one for 10 years, and two for 14 years. Four of the five colonies with exclosures were greater than 10 ha in area in 2012; the youngest colony was also the smallest at 1.87 ha. None of the colonies with prairie dog exclosures had a known history of agricultural tilling or were grazed by livestock during the study period. The temporary exclosures were
constructed with a wooden frame surrounded by metal poultry netting and staked to the ground to prevent movement. The poultry netting provided grazing access to smaller herbivores and invertebrates, but denied access to prairie dogs.

From the growing season of 2012 through the growing season of 2014, biomass clippings were conducted once a month from May through August, with the exception of 2012 when sampling stopped in July due to early plant senescence resulting from a lack of precipitation. For each sampling event, all vegetation within a 0.1 m$^2$ frame was clipped at a height of 1 cm above the soil surface from within each temporary exclosures as well as outside, 0.5 m away from the exclosure. Following biomass clipping, the exclosures were moved 1 m then secured to the ground. All clipped vegetation was dried at 60° C in a forced air oven for a minimum of 72 hours then air equilibrated prior to sorting by species and weighing. For all vegetation data, plant scientific names, origins (introduced or native), and functional groups (forb, grass, shrub, etc.), reported here follow nomenclature used by the USDA Plants Database (www.plants.usda.gov).

The ANPP of each exclosure was first calculated by subtracting the outside exclosure plant biomass from the paired inside exclosure biomass for every sampling month, then combining all monthly consumption values with the outside exclosure mass from the last month sampled into one ANPP value (McNaughton 1979, Fahey and Knapp 2007). In rare cases where there was more plant biomass outside the exclosure than within an exclosure for a sampling month, the monthly ANPP value was reported as zero. The ANPP of native grass, native forbs, introduced grass, and introduced forbs were quantified for each sampling year using the same procedure.

Data Analysis
To quantify the differences in sediment flux on prairie dog colonies and adjacent off-colony areas for each sampling month, analyses were conducted with linear mixed models (LMMs) utilizing the lme4 package (Bates et al. 2012) in R in order to account for the correlation caused by the sampling design. The model for each sample month included the fixed effects of prairie dog presence (binary variable), sample latitude, sample longitude, and the random effects of colony ID number (1-7). The latitude and longitude of the BSNE samplers were included to examine if spatial location had an effect on sediment flux. Prairie dog colony age was originally included as a fixed effect variable in the LMMs, based on the assumption that colony age would affect sediment flux rates. However, in every instance, incorporating the variable of colony age increased the model AIC value by more than 2 points, indicating poorer model fit. Therefore, prairie dog colony age was not included as a variable when modeling sediment flux.

Differences in TC and TN in the soil samples collected on and off prairie dog colonies were quantified with paired non-parametric Mann-Whitney U tests (or Wilcoxon signed-rank tests) in R. In order to determine the effect of prairie dog colony age on TC and TN, we first calculated TC loss and TN loss by subtracting the on colony TC and TN values from the off colony pair. If either TC or TN loss calculations resulted in a negative number, the value was changed to zero. We used linear models in R to quantify the relationship between TC loss and prairie dog colony age as well as TN loss and prairie dog colony age.

In order to examine the relationship between prairie dog colony age and the ANPP of different vegetation groups (e.g., all vegetation, native forbs, introduced forbs, native grasses, and introduced grasses), analyses were conducted with LMMs due to the correlation resulting from the exclosure sampling design. The models used to determine the effect of colony age on
the ANPP of specific vegetation groups included a fixed effect of prairie dog colony age and the random effects of sample year (2012-2014) and colony ID number (1-5).

To describe the differences in exclosure plant community composition resulting from prairie dog colony age, we examined the within-exclosure biomass of each plant species for each of the ten exclosures per site and grouped communities by colony age (5, 9, 11, and 15 years old). In our sampling design we measured the biomass of ten plots within the same site from 2012-2014, however more than one random effect (i.e., sampling year and site) cannot be accurately incorporated into an analysis of community data. Therefore, in order to compare plant communities based on colony age, we only examined plant biomass data from 2013. We utilized non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity to describe community differences based on the 2013 plant species biomass (Clarke 1993) among the four different colony ages with the vegan package (Oksanen et al. 2013) within R. Permutational Multivariate Analysis (PERMANOVA) of Bray-Curtis distances from the vegan package was used to test for significant clustering of Bray-Curtis values. To account for the error caused by sampling multiple plots within the same site, we used the site ID number as the group with which to constrain the PERMANOVA analysis. In order to examine exclosure community variance based on colony age, we utilized an analysis of multivariate homogeneity of group dispersions (BetaDisper) with the vegan package in R, which was run with permutation test, and results were compared with the Tukey’s HSD method.

**Results**

*Aeolian Sediment Flux*

Aeolian sediment flux on prairie dog colonies at the urban-wildland interface was significantly greater than sediment flux off colonies for 10 of the 12 months samples between
June 2014 and May 2015 ($P < 0.05$ for all; Fig. 4-1). For the sampling months of December 2014 and February 2015, there was no significant difference in sediment flux on and off prairie dog colonies ($P > 0.05$ for both). Throughout the entire study period, aeolian sediment flux on prairie dog colonies averaged 7.27 g m$^{-2}$ d$^{-1}$, while the off colony samplers average 0.84 g m$^{-2}$ d$^{-1}$. The time period containing the greatest on/off colony sediment flux disparity was in May 2015 when there was an average sediment flux of 18.78 g m$^{-2}$ d$^{-1}$ on prairie dog colonies and 1.55 g m$^{-2}$ d$^{-1}$ off colonies. BSNE sampler longitude had a significant effect on sediment flux in June 2014 only ($P = 0.045$); sampler longitude did not have a significant effect for the other 11 months that were sampled ($P > 0.05$ for all). BSNE sampler latitude did not have a significant effect on sediment flux for any of the 12 month sampled ($P > 0.05$ for all). In 2013, the aeolian sediment samples from prairie dog colonies contained an average TC of 4.46 (± 0.99) % and an average TN of 0.37 (± 0.08) %.

Fig. 4-1. Monthly sediment flux (in g m$^{-2}$ d$^{-1}$) collected from active prairie dog colonies and adjacent off-colony areas. Means ± SE are presented. * $P < 0.05$; ** $P < 0.01$
Soil Characteristics and Colony Age

The percent total carbon in the soil samples collected from the off colony areas (2.88 ± 0.26 %) was significantly greater than the on colony soil TC (2.06 ± 0.14 %; \( P < 0.01 \); Fig. 4-2A). Similarly, off colony soil percent total nitrogen (0.25 ± 0.02 %) was significantly greater than on prairie dog colony soil TN (0.19 ± 0.01 % \( P < 0.01 \); Fig. 4-2B). TC loss had no relationship with prairie dog colony age (\( P > 0.05 \)), however, TN loss increased significantly with increasing colony age (\( P < 0.05 \); Fig. 4-3).

Fig. 4-2. Boxplots demonstrating differences in total carbon (TC) in % mass and total nitrogen (TN) in % mass for on and off prairie dog colony soil samples. The bold horizontal lines indicate the median value, while the ends of the box correspond to the upper and lower quartiles. ** \( P < 0.01 \)
**ANPP and Colony Age**

There was no significant relationship between prairie dog colony age and ANPP ($P > 0.05$; Fig. 4-4); however colony age did have significant relationships with ANPP when examining plant species based on their origin and functional group. Introduced forb ANPP had a significant positive relationship with prairie dog colony age ($P < 0.001$; Fig. 4-5A), and increased from a mean of 19.5 ($\pm$ 5.3) g/m$^2$ on the four year old colony to an average of 323.3 ($\pm$ 40.6) g/m$^2$ on 16 year old prairie dog colonies. Conversely, the ANPP of native forbs, introduced grasses, and native grasses all had significant negative relationships with prairie dog colony age ($P < 0.05$ for all; Fig. 4-5A and 4-5B). Prairie dog colonies older than 12 years did not have mean ANPP values greater than zero for both the introduced or native grasses, indicating minimal grass growth on the oldest prairie dog colonies.
Prairie Dog Colony Age had dramatic effects on the plant community compositions that grew within the exclosures. When grouped by colony age, the exclosure plant communities were all significantly dissimilar from each other ($P < 0.001$ for all, stress = 0.09; Fig. 4-6).

Furthermore, community variability differed dramatically with prairie dog colony age. The youngest colony (5 years) contained significantly greater variability compared to all older colonies ($P < 0.05$ for all). Similarly, the two oldest colonies age groups (11 years and 15 years) had significantly less variability than the both the five and nine year old colonies ($P < 0.01$ for all). There was no difference in community variability between the 11 and 15 year old colony groups ($P > 0.05$).
Fig. 4-5. The relationship between prairie dog colony age (in years) and the ANPP (in g m^-2) of introduced and native forbs (A) as well as introduced and native grasses (B). Trend lines represent a significant ($P < 0.05$) change in ANPP with prairie dog colony age. Means ± SE are presented.
Fig. 4-6. Differences in plant community compositions based on prairie dog colony ages. Ellipses are 95% CIs. Stress = 0.09.

Discussion

As a native keystone species, prairie dogs in more natural prairie landscapes regulate important ecosystem services (e.g., Martínez-Estévez et al. 2013), and therefore play a critical role in the long-term suitability of grassland areas. However, recent research at the urban-wildland interface has shown that the presence of prairie dogs has elicited changes to plant community structure (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015), producing novel community compositions which may result in different ecosystem services than have been historically provided (Vitousek et al. 1987, Mack et al. 2001, Ehrenfeld 2003). This study
examined aeolian sediment emission rates, aboveground plant productivity, and soil fertility on prairie dog colonies within a complex modern landscape to quantify the effects of prairie dog occupation on ecosystem services in order to better understand the regulating role of prairie dogs at the urban-wildland interface.

Analysis of monthly aeolian sediment emission data shows higher aeolian sediment flux on prairie dog colonies at the urban-wildland interface compared to adjacent uncolonized areas. The temporal trends observed in the monthly aeolian sediment flux rates are consistent with other studies (e.g., Flagg et al. 2014) and are produced by a combination of biotic (i.e., vegetation and prairie dog activity) and abiotic (i.e., climate) factors. Colony plant cover peaks during the May-August growing season, but declines continually throughout the non-growing season due to constant prairie dog grazing. In contrast, adjacent off colony areas do not encounter the same level of vegetation loss, resulting in a higher cover of standing dead vegetation and litter throughout the year, directly decreasing wind erosion vulnerability on uncolonized areas. Additionally, prairie dogs in the study area have been observed vigorously digging for seedlings in the non-growing season leading to extensively pitted colony surfaces (Beals et al. 2015a). This behavior appears unique to the urban-wildland interface and presumably reduces topsoil stability. In addition to biotic factors, strong sustained winds typically occur in the region during the early-mid spring, so it was not surprising that this time period contained the highest monthly aeolian sediment flux rates. Although strong winds can also occur in the winter months, the presence of snow cover can prevent wind erosion regardless of wind speeds. In the winter of 2008-2009, high winds and an absence of snow cover in the study area resulted in dust storms emanating from prairie dog colonies that impacted adjacent highway traffic (Seastedt et al. 2013). Although we did not observe a reoccurrence of the 2008-
2009 colony winter dust storms during this study, potentially due to long periods of continuous snow cover, decreased snow precipitation in the region as predicted by current climate models (Knowles et al. 2006) could lead to an increased occurrence of colony winter dust storms in the future.

The results of this study clearly demonstrate that soil stability, an ecosystem service linked to the presence of prairie dogs in a more natural area (Martínez-Estévez et al. 2013), is not maintained at the urban-wildland interface. This does not suggest that the work by Martínez-Estévez et al. (2013) was inaccurate, but rather that in complex modern landscapes, prairie dogs are operating outside of their historical role due to the constraints imposed by humans. In a heavily anthropogenically-influenced landscape, prairie dog colony densities were found to be positively correlated with the level of restrictive anthropogenic features surrounding the colony (Johnson and Collinge 2004), which may lead to overgrazing and ultimately increasing bare soil voids and decreasing colony plant cover. Since areas of bare soil are vulnerable to wind erosion, it is not surprising the loss of plant cover on prairie dog colonies at the urban-wildland interface has resulted in higher aeolian sediment flux rates. Our findings are consistent with previous studies that have observed higher aeolian sediment flux from areas with large expanses of bare soil compared to areas with perennial grasses, shrubs, and other tall plants (Breshears et al. 2009, Munson et al. 2011, Flagg et al. 2014). It is clear that in a complex modern landscape, the presence of prairie dogs, a native keystone species, can no longer be associated with regulating soil erosion. Continued topsoil erosion could result in the subsoil, which contains a higher clay content, contributing more to the texture characteristics of the soil surface. The combination of increased bare soils on colonies (Beals et al. 2014) with changing soil texture, suggests a probable change to soil infiltration rates which could increase surface runoff, and represent an
additional modification to the ecosystem services associated with prairie dogs at the urban-wildland interface.

Prairie dog grazing has the ability to increase ANPP in less-anthropogenically disturbed grasslands (Holland et al. 1992, Martínez-Estévez et al. 2013); however, this can only be accomplished by maintaining soil fertility levels. The loss of topsoil nutrients through wind erosion has been shown to decrease plant productivity (Larney et al. 1994, Larney et al. 1998) and shift vegetation communities (Alvarez et al. 2012) in grassland areas. In the aeolian sediment samples collected from prairie dog colonies, the percent of TC (4.46 ± 0.99) and percent of TN (0.37 ± 0.08) were greater than the TC (1.81 ± 0.05) and TN (0.16 ± 0.003) values collected from pastureland soils in the same region (LeJeune et al. 2006), supporting the idea that the wind eroded material emanating from prairie dog colonies is nutrient rich (de Jong and Kachanoski 1988, Yan et al. 2013).

Based on the higher aeolian sediment flux that was observed on prairie dog colonies at the urban-wildland interface, and since the wind eroded material is likely fertile, the expectation would be for prairie dog colony plant productivity and soil fertility levels to decrease over time due to the continuous loss of nutrient rich topsoil. Although we observed less TC and TN on prairie dog colonies compared to adjacent off colony areas, only TN loss had a positive relationship with prairie dog colony age. Furthermore, the results of our study have shown that prairie dog colony age as measured here had no relationship with total ANPP, which seemingly conflicts with previous wind erosion research (e.g., Larney et al. 1994, Larney et al. 1998). However, our analysis showed ANPP declines for native forbs, native grasses, and introduced grasses with increasing colony age. In fact, the average ANPP of both native and introduced grasses were zero on colonies older than 12 years. Introduced forbs were the only plant group to
increase ANPP with prairie dog colony age, which was primarily driven by the proliferation of field bindweed, *Convolvulus arvensis*. This change from the fine root structure of historically common grass-dominated plant communities to the woodier and coarser root structure of *C. arvensis* is likely to have large impacts on soil C and soil fertility, changing the processes and functions of the colonized areas (e.g., Vitousek et al. 1987, Mack et al. 2001, Ehrenfeld 2003). While a decline in total ANPP on prairie dog colonies over time did not occur, as might be expected, the observed shift in plant community compositions away from grasses and towards introduced forbs suggests dramatic shifts in plant community compositions over time.

Analysis of plant community compositions based on colony age suggests that as prairie dog colonization duration increases at the urban-wildland interface, plant communities demonstrate a clear trajectory of change towards less variable compositions. While the presence of prairie dogs at the urban-wildland interface has been linked to lower plant diversity than adjacent uncolonized areas (e.g., Beals et al. 2014), there had been no comprehensive study examining the effect of colony age on community composition. This study has clearly shown that continued prairie dog colonization at the urban-wildland interface can transition a plant community from a highly variable and diverse community towards a less variable community that in some instances may resemble an introduced forb monoculture. Selective grazing appears to be the dominant mechanism driving prairie dog colony plant community shifts, however small aeolian sediment flux increases in arid grasslands decreased the cover of grasses and increased the cover of forbs (Alvarez et al. 2012). Although we have observed a similar pattern of decreased grasses and increased forbs on colonies over time in this study, quantifying the contributions of aeolian sediment flux compared to the selective grazing pressures of prairie dogs on plant community compositions was challenging and outside the scope of this study. However, if the
observations that increased aeolian sediment flux can shift plant community compositions (Alvarez et al. 2012) hold true in this system, then restoring historically common plant communities on prairie dog colonies at the urban-wildland interface will only become more complicated (Beals et al. 2015a, Beals et al. 2015b). Regardless, the fact that plant communities undergo shifts towards less variable compositions over time further emphasizes the need for land and wildlife managers operating at the urban-wildland interface to develop management strategies based on recent work conducted in complex modern landscapes. It is clear that research conducted in more natural prairie landscapes cannot be applied in a heavily anthropogenically-influenced landscape, and that the ecological role of prairie dog has changed due to constraints imposed by human development.

Forage biomass and aboveground productivity are vital ecosystem services for the long-term sustainability of prairie dog colonies and independent ranchers that use colony areas for cattle grazing. In the semi-arid grasslands of Northern Mexico, areas colonized by prairie dogs had significantly greater forage biomass (91.6 g/m²) compared to adjacent uncolonized grasslands (79.4 g/m²; Martínez-Estévez et al. 2013), suggesting that prairie dogs regulate forage biomass. Although we did not quantify biomass on adjacent uncolonized grasslands, a study conducted in an uncolonized grassland in Boulder County observed an average of 222.4 (± 19.4) g/m² of plant biomass from 2011-2012 (Prevéy et al. 2014), which is nearly double the 147.1 (± 11.2) g/m² of biomass was observed on prairie dog colonies from 2012-2014. However, our observation of prairie dogs decreasing plant biomass compared to uncolonized areas is not unique to the urban-wildland interface. Prairie dog colonies in Badlands National Park, South Dakota, USA, have been documented with less plant biomass compared to adjacent areas without prairie dogs (Fahnestock and Detling 2001). Based on the findings from all of these
studies, it appears that prairie dog colony plant productivity may be related to the specific ecosystem, landscape, and plant communities that are colonized. Landscape context plays a critical role in predicting the effects of prairie dogs on plant biomass, and should always be considered in order to avoid unexpected management outcomes.

While this research has focused on three ecosystem services and their relationship with the presence of prairie dogs at the urban-wildland interface, there are numerous other services that the presence of prairie dogs provides. For instance, many members of the general public enjoy viewing prairie dogs as native wildlife, which can promote conservation and biological education across age groups. The purpose of this research was not to advocate for prairie dog removal at the urban-wildland interface, but to increase our understanding of how humans have constrained the role of the prairie dog and what that entails for future sustainable management. Land and wildlife managers, as well as the general public, should be aware that our classical knowledge of prairie dogs and their effects on ecosystems cannot be applied without taking landscape context into consideration. Ultimately, it will be up to all public stakeholders, including ranchers and conservationists, to decide the goals of prairie dog management while understanding the changes that may occur.
CHAPTER 5
CONCLUSIONS

The ecological role of the black-tailed prairie dog has changed at the urban-wildland interface. This research has built upon previous studies demonstrating the negative impacts of prairie dogs on native grasslands along the Front Range (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015). I have shown that plant community restoration on prairie dog colonies at the urban-wildland interface, following either plague extirpations or management removal, has resulted in different outcomes than have been observed in more natural landscapes (Chapters 2 and 3). Furthermore, multiple ecosystem service benefits associated with the presence of prairie dogs in more natural landscapes, such as soil stability, increased aboveground plant productivity, and forage biomass regulation, are not maintained at the urban-wildland interface (Chapter 4). The findings of this research demonstrate the ability of a human-impacted landscape to change the historical role of a keystone species, and emphasize the effect that landscape context and human development can have on a native species’ ecological role.

Previous studies on plant community changes in natural areas resulting from prairie dog removal either via plague (Hartley et al. 2009, Augustine et al. 2014) or eradication (Osborn and Allan 1949) suggest that most plant characteristics on plague extirpated colonies were no different from adjacent off colony areas, and community recovery can occur in less than five years (Hartley et al. 2009, Augustine et al. 2014). Based in part on these findings, numerous management agencies at the urban-wildland interface have proposed prairie dog removal as a potential solution to minimize introduced plant proliferations, and ultimately reestablish the historical ecosystem function and services of colonized areas (e.g., City of Boulder Open Space and Mountain Parks 2010). However, prairie dog colonies at the urban-wildland interface contain
disparate abiotic conditions and biotic communities compared to colonies in more natural areas, which could present major obstacles for successfully restoring historically common communities (Hobbs et al. 2009, Suding and Hobbs 2009).

In order to understand prairie dog colony restoration at the urban-wildland interface, I examined the effects of both passive (i.e., plague epizootics) and active (i.e., management intervention) prairie dog removal on vegetation communities and plant species. Analysis of remote sensing data following plague extirpations at the urban-wildland interface suggests that passive prairie dog removal will not restore plant communities to historical compositions found on unoccupied areas, but rather allow for a potential proliferation of introduced winter active species and exotic forbs (Chapter 2). Similarly, three years of active prairie dog removal did not return plant communities, groups, or vegetation diversity to the levels equivalent to those found on uncolonized areas, and transitioned the restored communities to alternative compositions that were dissimilar from uncolonized grasslands (Chapter 3). Although removing prairie dogs for 3-5 years has successfully restored vegetation communities in more natural prairie landscapes, the lack of success that I observed at the urban-wildland interface can most likely be attributed to the novel plant compositions on colonies and the surrounding landscape. While prairie dog colonies in more natural systems exist in a matrix dominated by large areas of native vegetation, prairie dog colonies at the urban-wildland interface are surrounded by, at best, small patches of native vegetation. The reduced native seed source availability may slow native plant regeneration compared to natural areas, and therefore not meet the restoration goal within the same timeframe. Chapters 2 and 3 demonstrate that restoring novel plant communities by removing prairie dogs, either passively or actively, is potentially problematic due to the unexpected proliferations of non-native forbs and lack of native plant regeneration. This research provides a valuable example
to our understanding of novel community restoration, as well as emphasizing the role and effect of landscape context on ecosystems and their restoration.

Similar to our understanding of prairie dog colony restoration, the majority of our scientific knowledge linking the presence of prairie dogs to ecosystem services, such as soil stability and forage biomass regulation, has come from research conducted in more natural prairie landscapes (e.g., Holland et al. 1992, Martínez-Estévez et al. 2013). Many prairie dog advocates currently promote conservation management based on these findings, without considering landscape context. However, due to the link between plant community composition, ecosystem structure, and ecosystem function (e.g., Vitousek et al. 1987, Mack et al. 2001, Ehrenfeld 2003), the plant community shifts observed on colonies at the urban-wildland interface (Magle and Crooks 2008, Beals et al. 2014, Hopson et al. 2015) suggests the potential for prairie dogs to alter ecosystem level processes.

Analysis of monthly aeolian sediment flux showed nearly ten times the amount of wind eroded material emanating from prairie dog colonies compared to adjacent uncolonized areas, clearly demonstrating that soil stability is not regulated by prairie dogs at the urban-wildland interface (Chapter 4). Despite higher wind erosion rates, the plant aboveground net primary productivity (ANPP) on prairie dog colonies at the urban-wildland interface did not show declines with increasing colony age as would be expected with the continuous loss of nutrient rich topsoil (Larney et al. 1994, Larney et al. 1998). However, analysis of plant groups revealed that introduced forb ANPP increased with colony age, while the ANPP of native forbs, native grasses, and introduced grasses all declined. Furthermore, the percent of total carbon and nitrogen in surface soils collected from prairie dog colonies were less than the amounts observed in adjacent uncolonized areas, indicating lower soil fertility on colonies. This research has
demonstrated that multiple ecosystem service benefits associated with the presence of prairie dogs in more natural landscapes are not maintained at the urban-wildland interface.

The research for this dissertation has focused on prairie dog populations at the urban-wildland interface and has built upon studies by Magle and Crooks (2008), my Master’s research, and Beals et al. (2014). This work has operated under the assumption that low impact directional change drivers, such as climate change (e.g. Ray et al. 2008, Archer and Predick 2008), atmospheric chemistry changes (e.g., Baron 2002, Zelikova et al. 2014), and non-native species introductions (Lawton 2010), are driving grassland communities towards novel compositions over time and the presence of prairie dogs has amplified this trajectory of change towards novel compositions at rates faster than the low impact drivers alone (Beals et al. 2014). Based on these directional change assumptions, I hypothesized that time alone would result in community dissimilarities both within and between the uncolonized and colonized areas. For example, uncolonized plant communities in 1997 would be dissimilar from uncolonized communities surveyed in 2014. Furthermore, since prairie dog occupation at the urban-wildland interface can amplify the effects of low-impact drivers, I hypothesized that community dissimilarity would be maximized by a combination of prairie dog colonization with time.

To test the hypothesis that plant community compositions will show patterns (i.e., clustering) based upon the presence or absence of prairie dog colonization over time, I utilized plant community data from colonized and uncolonized areas in Boulder County sampled by City of Boulder Open Space and Mountain Parks (OSMP) personnel from 1997-2014. Since the data were collected as part of multiple research projects and management plans, and not designed to test my hypothesis, the data contained inconsistent sampling over time as well as an unbalanced sampling design (Table 4-1). In order to produce more standard sampling sizes across time, the
data were subset into two year groups, and transects were randomly selected to produce a more consistent sample size with each time group. In order to examine the effect of time on the colonized and uncolonized community compositions, the OSMP data were analyzed with the same methods I used Chapter 3: non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity among plots with the vegan package (Oksanen et al. 2013) within the statistical environment R (R Development Core Team 2008). In order to test for significant clustering of Bray-Curtis values, I used Permutational Multivariate Analysis of Variance (PERMANOVA) with Bray-Curtis distance matrices in R with the adonis function from the vegan package.

### Table 5-1. The number of uncolonized and colonized vegetation transects sampled by OSMP from 1997-2014.

<table>
<thead>
<tr>
<th>Year</th>
<th>Uncolonized Transects</th>
<th>Colonized Transects</th>
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<tbody>
<tr>
<td>1997</td>
<td>9</td>
<td>16</td>
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<tr>
<td>1998</td>
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<td>16</td>
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<td>2001</td>
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<td>42</td>
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<tr>
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<td>2011</td>
<td>26</td>
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<td>2014</td>
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The NMDS plots of the colonized and uncolonized plant communities did not show a clear trajectory of change over time (Fig. 4-1). In fact, the temporal community changes appeared more stochastic than I had expected, and therefore do not appear driven primarily by the low impact drivers as I originally hypothesized. Instead, the community changes from 1997-2014 presumably reflect seasonal climatic changes, such as temperature and precipitation, which would subsequently alter plant community compositions. To further illustrate that the observed community changes were not only the result of low impact directional drivers acting over time, the 1997-1998 colonized communities were most similar to the 2013-2014 colonized communities, when I hypothesized that these communities would be the most dissimilar.

Fig. 5-1. Changes in colonized (light grey) and uncolonized (dark grey) plant community compositions from 1997-2014. Dotted paths indicate the bi-annual directional change. Each symbol represents the average NMDS score for each treatment each year. Error bars omitted for clarity. Stress = 0.19 with all treatments.

Although the trajectory of change for the colonized and uncolonized communities over time did not meet the expectations of my hypothesis, the results of the PERMANOVA analysis
showed that the prairie dog colonized communities underwent five significant ($P < 0.05$) transitions from one time group to another, while the unoccupied areas only underwent two significant transitions ($P < 0.05$ for both). This finding suggests that the colonized areas are more likely to undergo significant changes over time compared to areas without prairie dogs. Although these findings are highly limited by the sampling design, they provide some insight into the processes driving plant community changes over time on prairie dog colonies and uncolonized grasslands in a complex modern landscape.

The findings of this research have revealed that the ecological role of the prairie dog has changed at the urban-wildland interface. Both passive and active restoration of colonized areas do not exhibit the desirable outcomes observed in more natural landscapes. Critical ecosystem services, such as soil stability, soil fertility, and forage biomass, are not regulated by prairie dogs at the urban-wildland interface. In total, these findings make it clear that sustainable grassland management decisions involving prairie dogs at the urban-wildland interface cannot be informed from previous studies conducted in more natural grassland areas. Land managers and the public cannot assume that the presence of prairie dogs at the urban-wildland interface will increase plant community diversity, stabilize soils, or increase forage biomass for grazers because these effects have been observed in other landscapes.

Increasing human development will result in changes to ecosystems, their function, and services; therefore, understanding these changes will be critical for future sustainable management. This dissertation research has shown that prairie dogs at the urban-wildland interface are operating outside of their historical context, and have the ability to dramatically impact grasslands ranging from plant community compositions to higher level ecosystem services. Land managers at the urban-wildland interface need to understand the impact that
prairie dogs and their conservation management can have on grasslands in order to sustainably manage these areas. The presence of prairie dogs has numerous ecosystem benefits and services that are independent from landscape context. For example in the Mid-Western U.S., prairie dogs are obligate prey for the endangered black-footed ferret (*Mustela nigripes*). Prairie dogs also provide opportunities for native wildlife viewing, which can promote conservation and biological education across age groups. The challenge going forward will be incorporate prairie dog management with sustainable grassland management decisions in order to maximize the benefits that these important areas provide.
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