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Resilience of a novel ecosystem after the loss of a keystone species: plague epizootics and urban prairie dog management

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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.

Key words: black-tailed prairie dogs; *Cynomys ludovicianus*; grasslands; introduced plants; novel ecosystems; resilience; restoration; urbanization.

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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% (1427 ha) of Boulder OSMP's total management area (17395 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 to 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*,

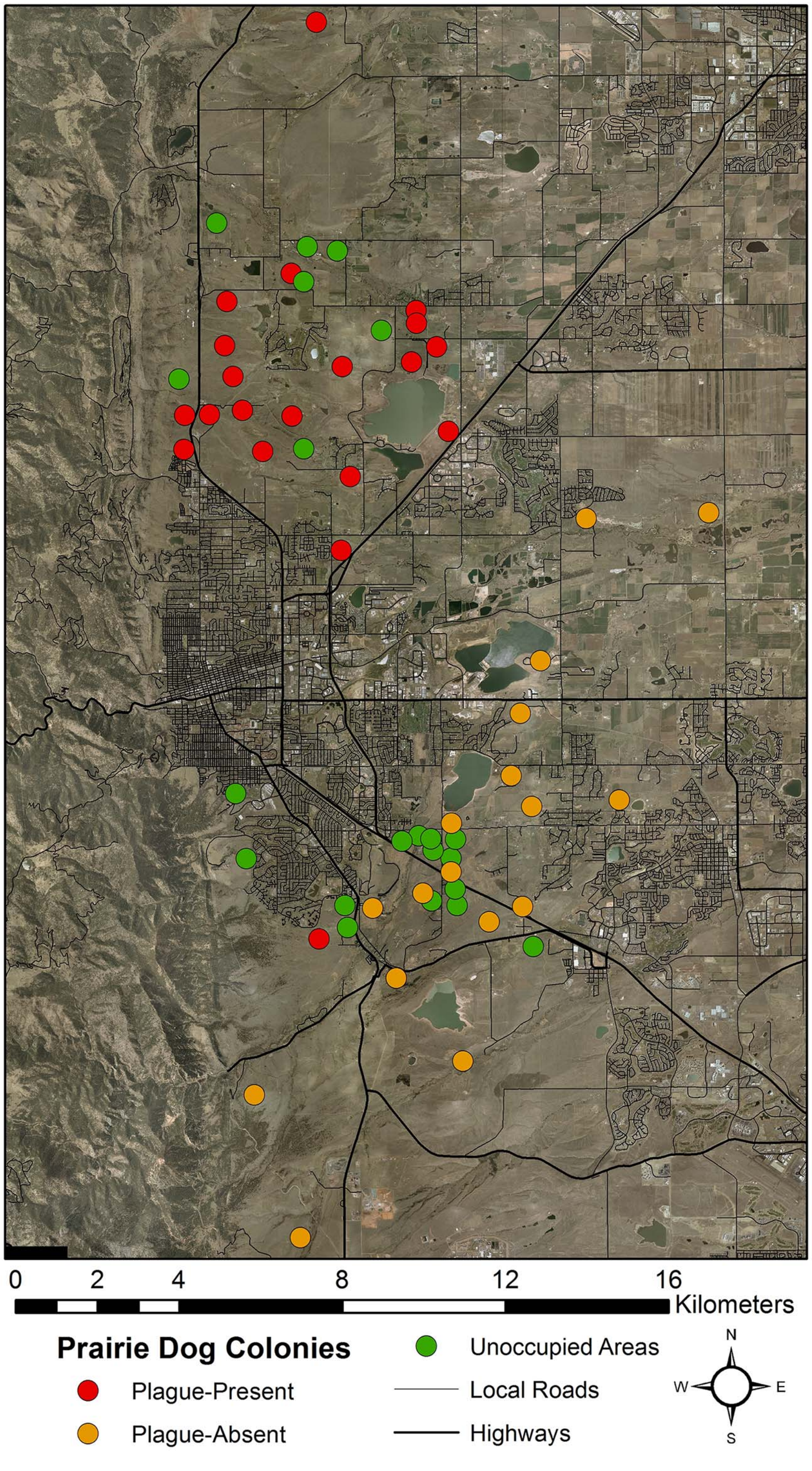

Fig. 1. Locations of plague-present prairie dog colonies ($n = 20$), plague-absent colonies ($n = 17$), and unoccupied areas ($n = 21$) on OSMP properties in Boulder, Colorado, USA (40°0′54″ N, 105°16′12″ W).

Bouteloua gracilis, and *Hesperostipa comate*, 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 preformed 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.

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 to 1996 (see Collinge et al. 2005), only six epizootics were documented on OSMP properties from 1996 to 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 to 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

$$\mathrm{SAVI} = \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + \rho_{red} + L} g(1 + L)$$

ρ_{NIR} and ρ_{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 m^2 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 to 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 and April), mid-season (May and June), and late season (July and 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 and 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 and April 2011 represent the only data available for that year's early-growing season.

The effect of plague epizootics on colony areas from 2004 to 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

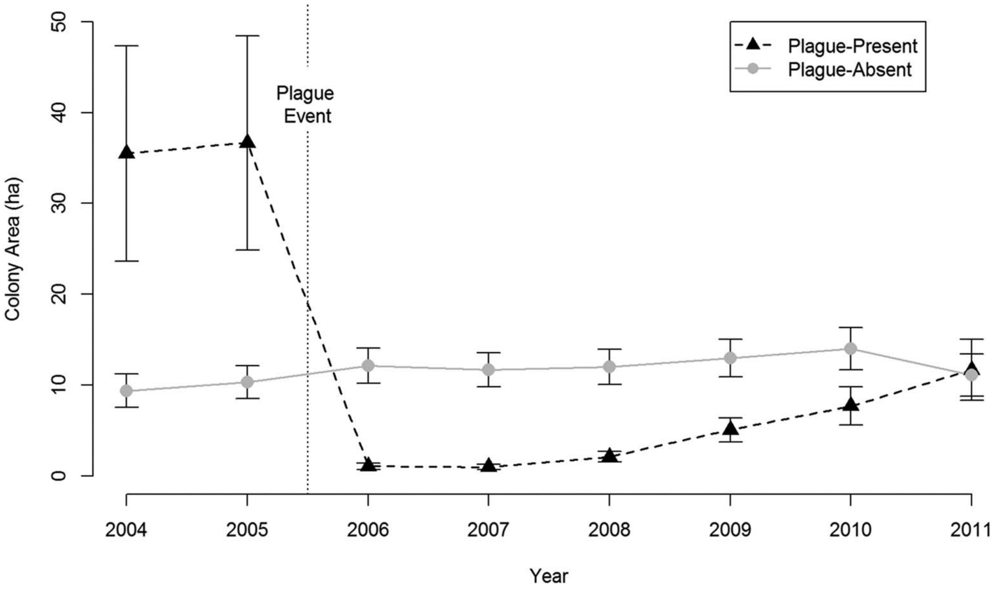

Fig. 2. Plague-present ($n = 20$) and plague-absent ($n = 17$) prairie dog colony areas (in ha) from 2004 through 2011. Mean ± SE are presented.

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 to 2011, two out of the 20 plague-present colonies remained extirpated in 2011. In contrast to the plague-present colonies, from 2004 to 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.

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 to 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 to 2007, as well as from 2009 to 2011, however, there was no significant difference in SAVI values between plague-present colonies

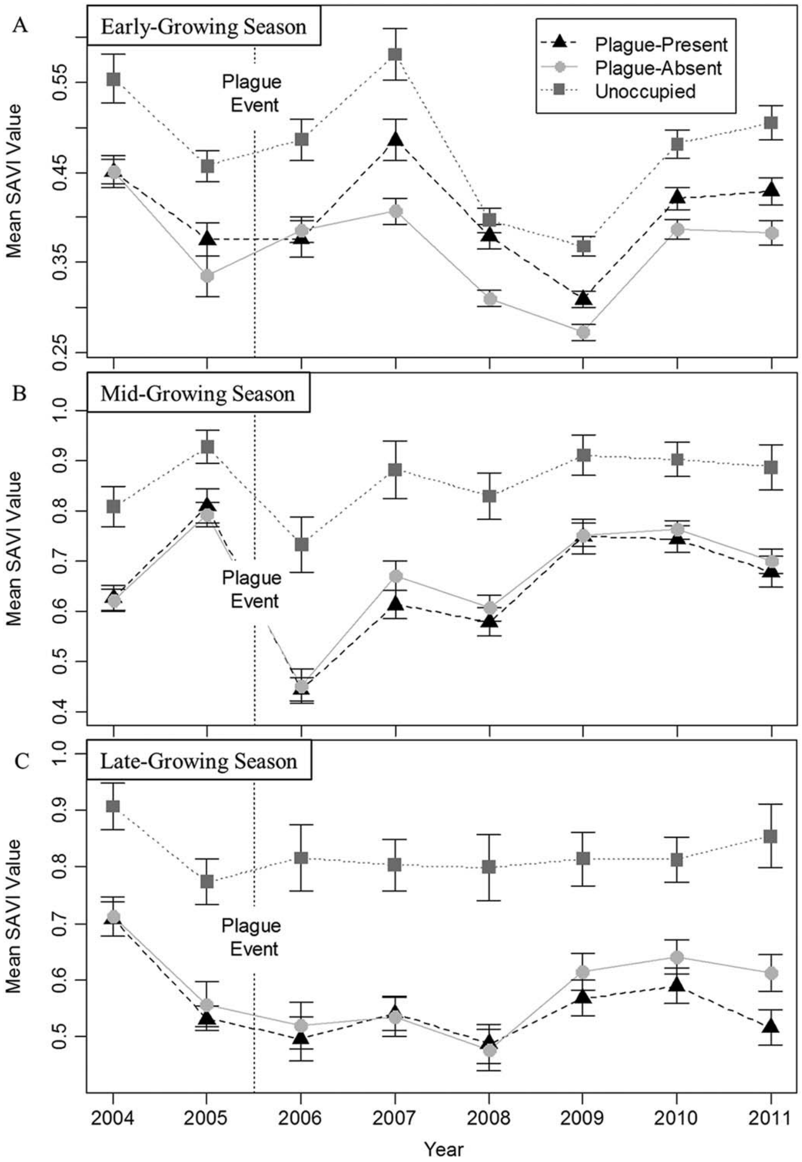

Fig. 3. Mean SAVI values for plague-present colonies ($n = 20$), plague-absent colonies ($n = 17$), and unoccupied areas ($n = 21$) from 2004 to 2011 for images from the growing season time subsets of early (A) mid (B) and late (C) growing season. Mean ± SE are presented.

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 to 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 to 2011 ($P > 0.05$ for all; Fig. 3B). The amount of green vegetation on the unoccupied areas in the mid-season from 2004 to 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 to 2010 ($P > 0.05$ for all; Fig. 3C); however in July and August 2011, SAVI

Table 1. Generalized linear mixed models of SAVI values for March and April 2004–2011 with fixed effect parameter estimates.

Model predictors of colony SAVI values	Fixed effect parameter	Model AIC_c	Model Akaike weight	Parameter estimate	SE
Plague epizootic					
	Intercept			0.372^{***}	0.022
	Plague epizootic			0.043^{***}	0.009
		−917.89	0.95		
Plague epizootic and historic tilling					
	Intercept			0.363^{***}	0.023
	Plague epizootic			0.043^{***}	0.009
	Historic tilling			0.021	0.019
		−911.02	0.05		
Plague epizootic, historic tilling, and colony size					
	Intercept			0.364^{***}	0.024
	Plague epizootic			0.042^{***}	0.009
	Historic tilling			0.021	0.019
	Colony size			0	0.000
		−891.36	0		

Note: *** $P < 0.001$.

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 to 2011 ($P < 0.05$ for all).

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 and August 2011.

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 above-ground green plant biomass, resulting in elevated early season SAVI values, as was observed on the plague-present colonies from 2007 to 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.

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