Chapter 15

CASE STUDY: ECOSYSTEM TRANSFORMATIONS ALONG THE COLORADO FRONT RANGE: PRAIRIE DOG INTERACTIONS WITH MULTIPLE COMPONENTS OF GLOBAL ENVIRONMENTAL CHANGE

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". . . in order to reliably predict the effects of global environmental change (GEC) on community and ecosystem processes, the greatest single challenge will be to determine how biotic and abiotic context alters the direction and magnitude of GEC effects on biotic interactions."

Tylianakis et al. 2008

Novel Ecosystems: Intervening in the New Ecological World Order, First Edition. Edited by Richard J. Hobbs, Eric S. Higgs, and Carol M. Hall.

15.1 INTRODUCTION

Biotic change in the 21st century is underway and is occurring via mechanisms that, because of their complexity, have been difficult for ecologists to encapsulate into general theory. At one extreme, biotic change is insidious, that is, slow change resulting from chronic low-intensity directional climate drivers interacting with relatively intact and resilient communities. The other endpoint involves the popularized 'tipping points' where the community rapidly transforms into a recognizably different state. As a terrestrial example, 'desertification' of the southwest is perhaps the best historical example of a rapid transition to a new community type (Schlesinger et al. 1990). These transformations can be the result of high-intensity short-duration events (drought, fire, overgrazing, etc.) acting alone, or the result of events operating on systems already undergoing responses to a suite of global environmental change factors.

In this chapter we describe a case study where a transformation is occurring as a result of events operating on a system already undergoing responses to a suite of global environmental change factors. In the Front Range of Colorado, intensive grazing by native black-tailed prairie dogs (*Cynomys ludovicianus*) in urban and suburban landscapes is interacting with climate change, nutrient deposition and non-native plant invasion to result in what we believe will be novel communities.

Responsible ecosystem stewardship demands that we understand – and hopefully predict – causal factors explaining the rate and trajectories of change (Chapin et al. 2010). Unfortunately, ecosystem complexity can result in 'ecological surprises' (Paine et al. 1998; Hastings and Wysham 2010) such as rapid die-back of forests in much of the Rocky Mountain region because of multiple sources of plant stress (Breshears et al. 2009). Paine et al. (1998) noted that multiple perturbations are sources of rapid changes, and that "understanding these . . . synergisms will be basic to environmental management decisions." Ecological surprises – and sometimes tipping points – can be generated directly by directional drivers but may, in particular, be facilitated when the drivers cause secondary (trophic level) impacts that amplify the direct effects. The opposite response is also possible (e.g. Post and Pedersen 2008) but, with the potential for invasive species to amplify trophic interactions, surprises should be expected.

Here we present an intriguing example of the ecological complexity initiated by global change factors. Within the framework of the environmental changes documented later, we identify mechanisms responsible for plant community change and how these mechanisms are influenced by the presence or absence of an important consumer, the black-tailed prairie dog.

Directional changes in climate and atmospheric chemistry are altering the environment of the Colorado Front Range, a region of increasing urbanization located at the junction of mountain foothills and mixed-grass to short-grass prairie. Among these directional changes are elevated average temperature (c. 2.5°F; Ray et al. 2008), higher rates of nitrogen deposition (Baron et al. 2000; Fenn et al. 2003), increased carbon dioxide concentrations (Morgan et al. 2007) and expansion of the length of the growing season (Archer and Predick 2008) are hypothesized and in some cases known to affect the distribution and abundance of grassland communities. These communities are perhaps more sensitive to changes than other systems because of the historical mix of species with C_3 or C_4 photosynthetic pathways that exhibit different CO_2, water and nitrogen (N) use efficiencies that in turn affect phenology and competitive interactions (e.g. Sage and Kubien 2003). In addition, these species evolved with a frequent fire return interval that has been suppressed by human activities. Since reduced fire intervals can enhance plant-available N on grassland sites and these sites are now exposed to perhaps an order of magnitude higher rate of inorganic N deposition than historical levels, the relative availability of this resource has been enhanced. Rapid-growing N-loving species clearly benefit from this change (e.g. Clark and Tilman 2008; Cherwin et al. 2009).

Growing season, as evidenced by remote sensing and a variety of phenological metrics, has expanded over the last decades (Myneni et al. 1997; Parmesan 2006; Kreyling 2010) and long-term records of flowering date in the western US show that spring blooms occur 2–3 days earlier per decade (Cayan et al. 2001). More recently, analysis of seasonal changes in northern hemisphere carbon dioxide concentrations indicates an expansion of the growing season of almost a month over the last 50 years (P. Tans, personal communication, 2005). These directional changes have occurred within the context of a temperate zone, continental climate that is characterized by very high interannual variability in precipitation (Knapp et al. 2001). Detection of directional changes can be further confounded by multiple decadal-scale oscillations in climate (Kitzberger et al. 2007).

A preliminary analysis of precipitation records indicates that no absolute changes in annual precipitation for the Front Range can be documented; however, winters are significantly wetter (Lawton 2010; J. Prevey, personal communication, 2012). The 110 year Boulder Colorado precipitation record indicates that the October–March 6 month interval produces an average of only 163 mm of 482 mm (34%) of annual precipitation. However, Lawton (2010) reported that the most recent 30 years of records had winter precipitation averaging 199 mm, 122% of the previous 70-year average. While climate change model predictions for this region contain high uncertainty regarding precipitation, the warming alone will alter the seasonality of plant water availability (Smith and Wagner 2006). Further, as monthly temperatures in Boulder now average above freezing year-round, the percentage of precipitation as snow is less and snow that does fall will likely melt rather than be retained for significant periods of time. Exactly how this affects plant water availability remains unstudied, but the exposed surface may allow for winter growth of cold-tolerant species.

The impacts of these cumulative environmental changes are intrinsically interesting and merit careful study. For example, the longer growing season and wetter winters appear to favor an increase in the abundance of winter annual plants (Lawton 2010). Among these, *Bromus tectorum* (cheatgrass) is best known. While introduced cheatgrass has long been a problem in the winter-wet Great Basin ecosystems of North America (Leopold 1949), its emergence onto the western edge of the Great Plains as a dominant species of this more summer-wet biome was unexpected and appears a recent phenomenon (Bush et al. 2007; Buckner and Downey 2009). The increase in winter annuals is believed to be a result of adequate or increased winter precipitation and increased nitrogen deposition, in addition to the expanded growing season.

These species have not been particularly successful at invading low-nutrient soils (Cherwin et al. 2009), but have done well in more fertile soil areas (Lawton 2010). Among the other common winter annuals are *Alyssum parviflorum* (annual peppergrass) and *Erodium cicutarium* (storksbill). Both of these are non-native annual forbs that appear to compete with the annual grasses for this new niche. Only a single native annual grass, Sixweeks fescue (*Vulpia octoflora*), is occasionally found in this group (Lawton 2010). Recent modeling efforts and a synthesis of existing literature suggest that soil-moisture-mediated competition and competitive exclusion are likely to occur between the winter annuals and native perennials (Everard et al. 2010). The presence of a new suite of cool-season-adapted species may therefore not only exploit a new resource opportunity, but also compete with the native species that would otherwise have benefited from the environmental changes.

The Front Range has also been the location for invasions by a number of C_3 (cool season) perennial species. Of these, *Convolvulus arvensis* (field bindweed) appears to become a dominant species within the community only when competition from other common plant species is severely reduced. Until recently this species was regarded as an agricultural weed, one that exploited disturbance and high nutrient availability, but was not a concern in less-disturbed areas. One mechanism that facilitates dominance by bindweed and other introduced plants is grazing and burrowing by *Cynomys ludovicianus*, the black-tailed prairie dog (Magle and Crooks 2008). Prairie dogs are identified as keystone species and have been discussed for potential listing as threatened and endangered, yet they have facilitated winter dust storms at numerous sites along the Colorado Front Range (Figs 15.1 and 15.2). High densities of prairie dogs in the past, even under drought conditions, did not produce documented winter dust storms. This phenomenon was not known to occur prior to the increased dominance of invasive plant species in the Colorado Front Range. One interpretation is that we are observing the first stages of a catastrophic regime shift (e.g. Scheffer and Carpenter 2003) similar to the desertification phenomenon observed in the Southwest (Schlesinger et al. 1990).

Prairie dogs are common within the grassland remnants found along the Colorado Front Range. These animals have been intensively studied elsewhere due to their ability to perform as keystone species (Wiens 2009), maintain grasslands (Weltzin et al. 1997) and function as ecosystem engineers (Kotliar et al. 1999; VanNimwegen et al. 2008). The black-tailed prairie dog in particular has been well studied because of its widespread dominance or former dominance in the mixed- and short-grass prairie region of the Great Plains, and because the species has been perceived as a competitor with cattle (Whicker and Detling 1988; Derner et al. 2006; Wiens 2009). Its impacts on vegetation in both natural areas (e.g. Fahnestock and

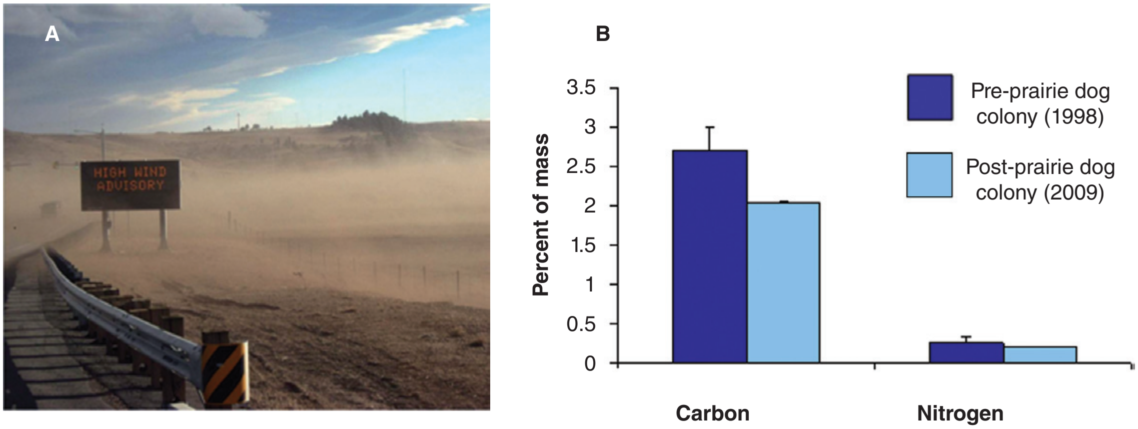

Figure 15.1 A. (a) Dust emissions from prairie dog colony south of Boulder, CO, 7 January 2009 causes a highway hazard (courtesy of US Geological Survey). This photo was published on the cover of the October 2010 issue of *Frontiers in Ecology and the Environment*. (b) Total carbon and nitrogen content of top 10 cm of soil measured before and after the site experienced substantial soil erosion.

Figure 15.2 Left: a native prairie occupied by prairie dogs for a decade as seen in September 2008. Center: by spring 2009 most plant cover was gone and severe wind erosion was noted. Right: plague removed the colony by late spring 2009, resulting in a meadow of native fringed sage (*Artemesia frigida*), annual sunflowers (*Helianthus* sp.) and non-native bindweed (*Convovulus arvensis*).

Detling 2002) and at the urban interface (e.g. Magle and Crooks 2008) are well known.

The wealth of studies that have been produced by Detling and colleagues since the 1980s confirm a consistent pattern of impacts produced by this species (e.g. Whicker and Detling 1988; Fahnestock and Detling 2002; Hartley et al. 2009). First, aboveground production appears largely unchanged despite very large changes in community composition, with a decrease in the absolute and relative abundance of the grasses and an increase in herbaceous dicots (forbs). In both short- and mixed-grass prairies, the effects of prairie dog grazing on plant community composition increases with the length of time the area is occupied. Individual prairie dog colonies shift spatially on the landscape over time, with the result being that long-term grazed

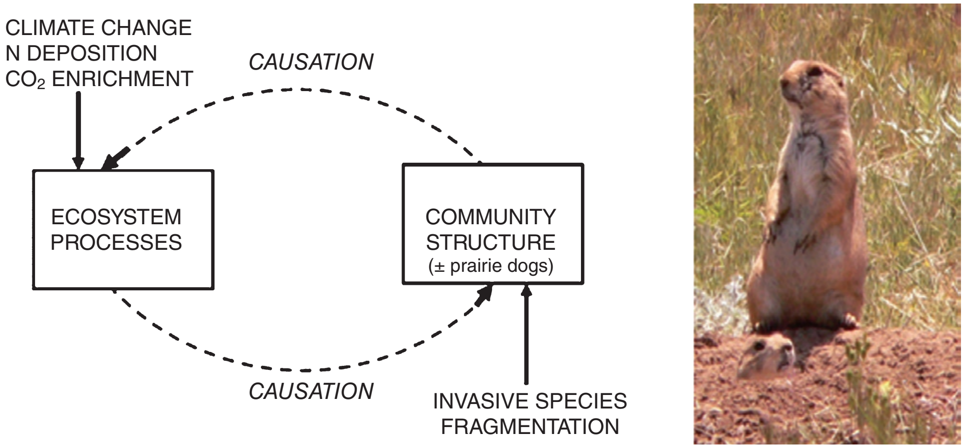

Figure 15.3 New plant species and a new environment form communities that interact with and modify grazing intensity by prairie dogs (courtesy of Mark Bradford); cheatgrass is the dominant plant cover.

areas are periodically abandoned (Augustine et al. 2008). Now, however, with habitat fragmentation in the Front Range and lack of acceptable adjacent habitats, the animals may remain on areas for longer time intervals. As prairie dog colonies become more static, these animals engineer habitats dominated by mostly non-native forb and shrub species (Fig. 15.3). Until very recently however, these changes had not caused large-scale erosion events. Further, we observed colonies to remain on heavily impacted areas even though sites were not bounded by any human or natural barriers to dispersal. The animals may prefer remaining on what appear to be degraded habitats rather than invade adjacent grasslands.

Prairie dogs have been discussed for federal listing as an endangered species (Kotliar et al. 1999) yet their presence is a concern at the urban–wildland interface, particularly in the Colorado Front Range. These animals form unusually high densities adjacent to urban areas (Johnson and Collinge 2004) and in particular appear to overgraze areas that have been restored from agricultural lands. In 2006, a restored grassland site in Fort Collins, Colorado experienced extensive wind erosion on areas colonized by prairie dogs such that the animals were removed and the site proactively restored. In the winter of 2008/2009, four similar areas in Fort Collins were affected (Pankratz 2009). Similar dust storms began on prairie dog colonies in the prairies surrounding the Boulder area in 2008/2009 and included sites that had been restored as well as native prairie areas.

Prairie dogs do not hibernate, but they greatly restrict their foraging activities during cold weather. This behavior presumably results from the fact that energy loss is reduced by staying in burrows rather than attempting to forage senescent vegetation under cold temperatures. Exactly how the duration and intensity of foraging has been influenced by the longer growing season and by a change in food quality (available energy and protein content) of the senescent vegetation in this region also remains unknown, but we believe that prairie dogs now use invasive species for grazing during the non-growing season in ways that contribute to the denudation of the landscape. While quantitative studies are lacking, the observations of either only non-native vegetation or essentially no vegetation on colonies attests to a transformation from historical patterns.

The lack of vegetation cover on prairie dog colonies in and adjacent to urban areas in mid-winter now appears to cause wholesale wind and water erosion of mixed-grass prairie in some years. This change appears well beyond the reduction in cover and increased forb abundance reported for prairie dog colonies of native prairie in earlier studies (Fahnestock and Detling 2002), or the erosion caused by isolated prairie dog mounds. This is a new phenomenon with wholesale implications for biodiversity and ecosystem services of these areas, i.e. the generation of novel ecosystems (Hobbs et al. 2006, 2009; Seastedt et al. 2008). The 'new' dynamics caused by the interactions of fragmentation, climate change and invasive species are hypothesized to convert a keystone species into an ecosystem transformer, and shift perennial grasslands to shrublands and landscapes dominated by non-native forbs (Fig. 15.4).

In the fall of 2008, several prairie dog colonies in Boulder County were observed that consisted largely of recently germinated annual plants accompanied with senescent fields of bindweed. By spring, these areas were devoid of vegetation. Soils were resampled at one site that had been part of a vegetation study in 1999, and the top 10 cm of soils had lost 25% of their organic C and N over the time period (Fig. 15.1b). The dust storms did not reoccur in 2009/2010 due to less wind, the presence of snow cover during much of the winter and the fact that the plague decimated many prairie dog colonies. Ironically, plague (*Yersinia pestisi*) is a disease accidentally introduced from Eurasia in the last century (Antolin et al. 2002), but its recurrence in the Front Range now appears to be the mechanism providing some persistence in vegetation diversity and dynamics because colony areas are periodically relieved of grazing pressure when plague epizootics occur (Hartley et al. 2009). Studies underway at the University of Colorado (L. Sackett, personal communication, 2012) suggest that resistance to the plague may be developing in the prairie dog species. In any event, the majority of colonies in our area already appear to be recovering from a current cycle of plague that began in Boulder County in 2006. By the winters of 2010/2011 and 2011/2012, minor dust storms were again being generated from colonies in the area.

The dialog about protecting prairie dogs as endangered species is ongoing, but the dialog about protecting ecosystem services provided by the prairie dogs within the realities imposed by global environmental change has yet to be initiated. While we confirm the scientific consensus that prairie dogs are critically important species in grasslands (Wiens 2009), we also believe that failing to recognize how this species interacts with new climate regimes and new plant species causes additional conservation problems. This problem is viewed as a model system of how trophic interactions can interact with global environmental change drivers to produce novel outcomes not predicted by climate drivers alone (Paine et al. 1998; Suttle et al. 2007). The concept of 'keystone species' in an era of rapid

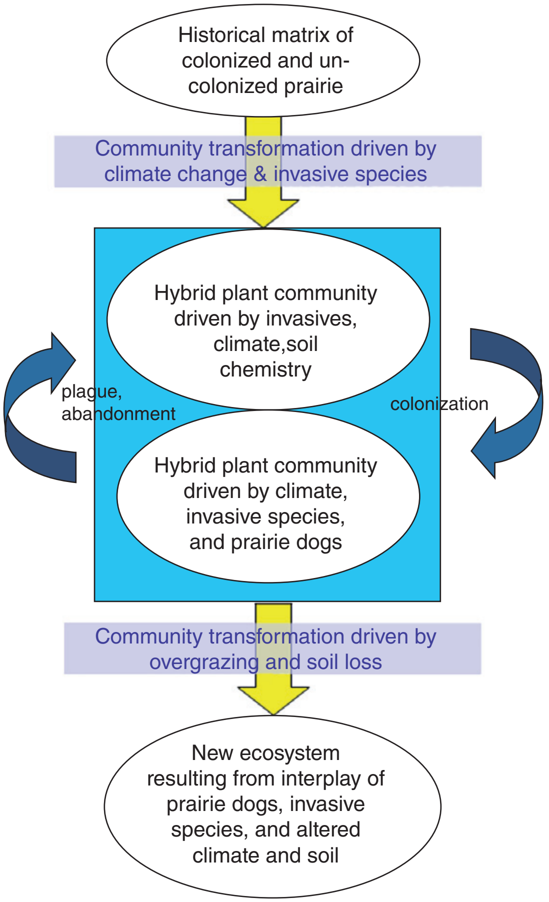

Figure 15.4 The short- and mixed-grass prairies of the Colorado Front Range are diverging from their historical configuration, with prairie dogs altering soils in ways that favor species that historically were only minor components of the vegetation. Colonization (a relatively slow process) and colony removal by plague (a rapid transformation) and abandonment connect the two new systems, but return to the historical grasslands is not viewed as a viable option. Once prairie dogs have created novel communities, their legacy effects on sites that are 'plagued out' may differ significantly from sites only impacted by invasive species. The yellow arrows are viewed as 'points of no return' (without large amounts of human intervention) but the second conversion to an eroded landscape more common to the southwestern US remains uncertain.

environmental change may require revision. Second, and as already noted by Hartley et al. (2009), the ability of prairie dogs to continue to function in their historical context now appears to be regulated by decadal-scale plague outbreaks. Ironically, the traditional ecological functions (i.e. the graminoid-forb cycles generated by prairie dogs; Whicker and Detling 1988; Fahnestock and Detling 2002) as well as the creation of critical habitat for species such as burrowing owls (which use the abandoned prairie dog burrows), are now being maintained by an introduced pathogen. While we need to find a more benign alternative to plague, this disease now appears to be a management aid (at least at the urban–wildlands interface where reintroduction of keystone predators such as ferrets is unlikely to be a viable management option).

Expansion of urban, suburban and exurban areas on the Front Range of Colorado continues to replace agricultural lands. However, the permanent grassland holdings by federal, county and local governments consist of many thousands of hectares and will remain a significant percentage of this landscape. Conflicts of use and management along the urban–wildland interface that have large impacts on the ecological services and conservation values of these lands are common and, as indicated here, are increasing. We see this example as a model system to engage educators, managers, policy makers and stakeholders in a dialog for developing sustainability strategies for the Colorado Front Range (Chapin et al. 2010). The science provided by this study should inform the dialog required for decisions to 'manage for resilience' versus 'manage for change' and for considering the values and consequences of new ecosystem states (West et al. 2009). As noted by Chapin et al. (2010), there exists a compelling need to have "researchers and managers collaborate through adaptive management to create continuous learning loops". The current interactions among prairie dogs, new plant species and other global environmental change factors provide a compelling and relevant focus for such a learning activity.

ACKNOWLEDGMENTS

The study of interactions between climate-invasive plant species and prairie dogs was supported by the National Science Foundation grant, DEB-1120390.

REFERENCES

Antolin, M.F., Gober, P., Luce, B., Biggins, D.E., Van Pelt, W.E., Seery, D.B., Lockhart, M. and Ball, M. (2002) The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. *Transactions of the North American Wildlife and Natural Resources Conference*, **67**, 104–128.

Archer, S.R. and Predick, K.I. (2008) Climate Change and Ecosystems of the Southwestern United States. *Rangelands*, **30**, 23–28.

Augustine, D.J., Dinsmore, S.J., Wunder, M.B., Dreitz, V.J. and Knopf, F.L. (2008) Response of mountain plovers to plague-driven dynamics of black-tailed prairie dog colonies. *Landscape Ecology*, **23**, 689–697.

Baron, J.S., Rueth, H.M., Wolfe A.M. et al. (2000) Ecosystem responses to nitrogen deposition in the Colorado Front Range. *Ecosystems*, **3**, 352–368.

Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G. and Pockman, W.T. (2009) Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*, **7**, 885–189.

Buckner, D. and Downey, S. (2009) Patterns of annual brome abundance in reclaimed and native rangelands in the northern Great Plains: a case study from the Big Sky Mine, southeastern MT, in *Revitalizing the Environment: Proven Solutions and Innovative Approaches May 30–June 5, 2009* (ed. R.I. Barnhisel), National Meeting of the American Society of Mining and Reclamation, Billings, MT: Published by ASMR, 3134 Montevista Rd. Lexington KY.

Bush, R.T., Seastedt, T.R. and Buckner, D. (2007) Plant community response to the decline of diffuse knapweed in a Colorado grassland. *Ecological Restoration*, **25**, 169–174.

Cayan, D.R., Kammerdiener, S.A., Dettinger, M.D., Caprio, J.M. and Peterson, D.H. (2001) Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society*, **82**, 399–415.

Chapin, F.S., Carpenter, S.R., Kofinas, G.P. et al. (2010) Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends in Ecology and Evolutionary Biology*, **25**, 241–49.

Cherwin, K.L., Seastedt, T.R. and Suding, K.N. (2009) Effects of nutrient manipulations and grass removal on cover, species composition, and invasibility of a novel grassland in Colorado. *Restoration Ecology*, **17**, 818–826.

Clark, C.M. and Tilman, D. (2008) Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, **451**, 712–715.

Derner, J.D., Detling, J.K. and Antolin, M.F. (2006) Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment*, **4**, 459–464.

Everard, K., Seabloom, E.W., Harpole, W.S. and de Mazancourt, C. (2010) Plant water use affects competition for nitrogen:

why drought favors invasive species in California. *American Naturalist*, **175**, 85–97.

Fahnestock, J.T. and Detling, J.K. (2002) Bison-prairie dog-plant interactions in a North American mixed-grass prairie. *Oecologia*, **132**, 86–95.

Fenn, M.E., Baron, J.S., Allen, E.B. et al. (2003) Ecological effects of nitrogen deposition in the western United States. *BioScience*, **53**, 404–420.

Hartley, L.M., Detling, J.K. and Savage, L.T. (2009) Introduced plague lessens the effects of an herbivorous rodent on grassland vegetation. *Journal of Applied Ecology*, **46**, 861–869.

Hastings, A. and Wysham, D.B. (2010) Regime shifts in ecological systems can occur with no warning. *Ecology Letters*, **13**, 464–472.

Hobbs, R.J., Arico, S., Aronson, J. et al. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Hobbs, R.J., Higgs, E. and Harris, J.A. (2009) Novel ecosystems and their implications for conservation and restoration. *Trends in Ecology and Evolutionary Biology*, **24**, 599–605.

Johnson, W.C. and Collinge, S.K. (2004) Landscape effects on black-tailed prairie dog colonies. *Biological Conservation*, **115**, 487–497.

Kitzberger, T., Brown, P.M., Heyerdahl, E.K., Swetnam, T.W. and Veblen, T.T. (2007) Contingent Pacific-Atlantic Ocean influence on multi-century wildfire synchrony over western North America. *Proceedings of the National Academy of Sciences*, **104**, 543–548.

Knapp, A.K., Briggs, J.M. and Koelliker, J.T. (2001) Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems*, **4**, 19–28.

Kotliar, N.B., Baker, B.W., Whicker, A.D. and Plumb, G. (1999) A critical review of the assumptions about the prairie dog as a keystone species. *Environmental Management*, **24**, 177–192.

Kreyling, J. (2010) Winter climate change: a critical factor for temperate vegetation performance. *Ecology*, **91**, 1939–1948.

Lawton, W.C. (2010) Global environmental change factors and noxious weed management shape a novel grassland ecosystem on the Colorado Front Range. MSc thesis, University of Colorado, Boulder.

Leopold, A. (1949) *A Sand County Almanac*. Oxford University Press, Oxford.

Magle, S.B. and Crooks, K.R. (2008) Interactions between black-tailed prairie dogs (Cynomys ludovicianus) and vegetation in habitats fragmented by urbanization. *Journal of Arid Environments*, **72**, 238–246.

Morgan, J.A., Milchunas, D.G., LeCain, D.R., West, M. and Mosier, A.R. (2007) Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in shortgrass steppe. *Proceedings of the National Academy of Science*, **104**, 14724–14729.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. and Nemani, R.R. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.

Paine, R.T., Tegner, M.J. and Johnson, E.A. (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535–545.

Pankratz, H. (2009) Fort Collins plans prairie dog cull. *Denver Post*. http://www.denverpost.com/news/ci_11689469, Accessed August 2012.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Post, E. and Pedersen, C. (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of National Academy of Sciences*, **105**, 12353–12358.

Ray, A.J., Barsugli, J.J., Averyt, K.B., Wolter, K., Hoerling, M., Doesken, N., Udall, B. and Webb, R.S. (2008) Climate change in Colorado. A report to the Colorado Water Conservation Board. URL: http://wwa.colorado.edu/CO_Climate_Report/index.html (accessed August 2012).

Sage, R.F. and Kubien, D.S. (2003) Quo vadis C_4? An ecophysiological perspective on global change and the future of C_4 plants. *Photosynthesis Research*, **77**, 209–225.

Scheffer, M. and Carpenter, S.R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, **18**, 648–656.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huennke, L.F., Jarrell, W.M., Virginia, R.A. and Whitford, W.G. (1990) Biological feedbacks in global desertification. *Science*, **8**, 1043–1048.

Seastedt, T.R., Hobbs, R.J. and Suding, K.N. (2008) Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment*, **6**, 547–553.

Smith, J.B. and Wagner, C. (2006) Climate change and its implications for the Rocky Mountain region. *Journal of the American Water Works Association*, **98**, 80–92.

Suttle, K.B., Thomsen, M.A. and Power, M.E. (2007) Species interactions reverse grassland responses to climate change. *Science*, **315**, 640–642.

Tylianakis, J.M., Didham, R.K., Bascompte, J. and Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

VanNimwegen, R.E., Kretzer, J. and Cully, J.F. (2008) Ecosystem engineering by a colonial mammal: how prairie dogs structure rodent communities. *Ecology*, **89**, 3298–3305.

Weltzin, J.F., Archer, S. and Heitschmidt, R.K. (1997) Small mammal regulation of vegetation structure in a temperate savanna. *Ecology*, **78**, 751–763.

West, J.M., Julius, S.H., Kareiva, P., Enquist, C., Lawler, J.J., Petersen, B., Johnson, A.E. and Shaw, M.R. (2009) US natural resources and climate change: concepts and approaches for management adaptation. *Environmental Management*, **44**, 1001–1021.

Whicker, A.D. and Detling, J.K. (1988) Ecological consequences of prairie dog disturbances. *Bioscience*, **38**, 778–785.

Wiens, J.A. (2009) Landscape ecology as a foundation for sustainable conservation. *Landscape Ecology*, **24**, 1053–1065.