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Essay

Plague bacterium as a transformer species in prairie dogs and the grasslands of western North America

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Abstract: *Invasive transformer species change the character, condition, form, or nature of ecosystems and deserve considerable attention from conservation scientists. We applied the transformer species concept to the plague bacterium* Yersinia pestis *in western North America, where the pathogen was introduced around 1900.* Y. pestis *transforms grassland ecosystems by severely depleting the abundance of prairie dogs (*Cynomys spp.*) and thereby causing declines in native species abundance and diversity, including threatened and endangered species; altering food web connections; altering the import and export of nutrients; causing a loss of ecosystem resilience to encroaching invasive plants; and modifying prairie dog burrows.* Y. pestis *poses an important challenge to conservation biologists because it causes trophic-level perturbations that affect the stability of ecosystems. Unfortunately, understanding of the effects of* Y. pestis *on ecosystems is rudimentary, highlighting an acute need for continued research.*

Keywords: *Cynomys*, ecosystem function, invasive species, trophic perturbations, *Yersinia pestis*

La Bacteria de la Peste como una Especie Transformadora en los Perritos de las Praderas y los Pastizales del Oeste de Norteamérica

Resumen: *Las especies invasoras transformadoras cambian el carácter, la condición, la forma o la naturaleza de los ecosistemas y merecen atención considerable por parte de los científicos de la conservación. Aplicamos el concepto de especie transformadora a la bacteria de la peste* Yersinia pestis *en el oeste de Norteamérica, en donde el patógeno fue introducido alrededor de 1900.* Y. pestis *transforma los ecosistemas de pastizal al disminuir severamente la abundancia de los perritos de las praderas (*Cynomys spp.*) y por lo tanto causa declinaciones en la abundancia y diversidad de las especies nativas, incluidas las especies amenazadas y en peligro; altera las conexiones de las redes alimenticias; altera la importación y exportación de nutrientes; causa la pérdida de resiliencia del ecosistema ante las plantas invasoras; y modifica las madrigueras de los perritos.* Y. pestis *es un reto importante para los biólogos de la conservación ya que causa perturbaciones de nivel trófico que afectan la estabilidad de los ecosistemas. Desafortunadamente, el entendimiento de los efectos de* Y. pestis *sobre los ecosistemas es rudimentario, lo que resalta una necesidad aguda de investigación continua.*

Palabras Clave: especies invasoras, función del ecosistema, perturbaciones tróficas, *Cynomys*, *Yersinia pestis*

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Introduction

Management and control of invasive species are some of the most important challenges facing conservation scientists today (Ehrenfeld 2010; Simberloff & Rejmánek 2011). In particular, some invasive species change the character, condition, form, or nature of ecosystems over a substantial area of the ecosystems they affect. Instead of denoting these species simply as invasive, Richardson et al. (2000) proposed use of the term "transformer species" (in relation to plants) and suggested these species deserve considerable attention from conservation biologists.

The transformer species concept was recently extended from plants, and opportunities exist for further expansion (Ehrenfeld 2011). For example, although not yet discussed relative to the transformer species concept, disease-causing pathogens can invade and, once established, influence ecosystems via direct effects on susceptible native species and indirect effects on trophic relationships (Selakovic et al. 2014), as demonstrated by the introduction of rinderpest to Africa (Thomas et al. 2005; Dobson et al. 2011).

We extended the transformer species concept to *Yersinia pestis*, an exceptionally lethal, primarily flea-borne bacterium that causes plague in mammals. It has received much attention as a human pathogen, an emerging disease, and a potential agent of bioterrorism (Orent 2004). However, *Y. pestis* has received little attention in recent reviews of invasive species (Lowe et al. 2000) or the effects of invasive species on ecosystems (Pimentel et al. 2000, 2001, 2005; Simberloff & Rejmánek 2011).

Y. pestis was introduced to North America in 1900 when steamships from Asia ferried flea-infested rats to the U.S. Pacific coast (Orent 2004). In the next few years, epidemiologists quickly noted that *Y. pestis* had established itself in populations of peridomestic rats and free-ranging rodents in California (Eskey & Haas 1940). Efforts were made to eradicate plague, but the attempts were futile and *Y. pestis* spread to a broad range of mammalian hosts, especially rodents of the families Cricetidae, Muridae, and Sciuridae (& their fleas) (Gage & Kosoy 2005).

As early as the 1920s, ecologists recognized plague as a disease that can spread explosively across vast areas, and the implications of plague for wildlife were discussed. In his seminal papers on disease ecology, Charles Elton (1925, 1931) emphasized plague as a disease that could regulate rodent populations. Furthermore, Elton (1933, 1958) discussed plague in his classic book on the ecology of animals in 1933 and later in his book on invasive species in 1958. By the time Elton's book on invasive species was published, less than 60 years after *Y. pestis* was introduced to North America, the plague bacterium was entrenched in populations of mammals in 17 western United States, where the pathogen is now resident and occasionally spills over to humans (Barnes 1993).

Concepts of Invasive and Transformer Species Relative to *Y. pestis* in Western North America

The process of biological invasion occurs in 3 phases (Richardson et al. 2000): introduction, naturalization, and dispersal. During the introduction phase, humans help an organism overcome a major geographical barrier that is insurmountable without human assistance. In the naturalization phase, without barriers to population establishment, replication, and continued persistence, an introduced organism is naturalized. In the dispersal phase, the actual invasion occurs when the introduced species spreads geographically as it overcomes "barriers to dispersal within the new region" and copes "with the abiotic environment and biota in the general area" (Richardson et al. 2000:99).

For *Y. pestis* to be categorized as a transformer species, it must first be categorized as an invasive species. In western North America, *Y. pestis* overcame the Pacific Ocean with human assistance and was introduced to San Francisco (among other places), naturalized itself at introduction sites, and invaded western North America, causing dramatic declines in some mammal populations. *Y. pestis* invaded North America very quickly, spreading more than 2200 km in 40 years (Adjemian et al. 2007).

To be categorized as a transformer species, *Y. pestis* must affect a substantial area of ecosystems. This outcome seems most plausible in those cases in which plague reduces populations of a keystone species whose ecological impact is disproportionately unique relative to its abundance (Power et al. 1996), as is the case with species of *Cynomys* prairie dogs (Kotliar et al. 2006).

Prairie Dogs, Plague, and the Grasslands of Western North America

Prairie dogs are colonial burrowing rodents that serve as prey for many predators, create subterranean burrows used by many species, and clip and forage on vegetation in ways that facilitate forbs whereas reducing shrub encroachment (Hoogland 1995). Due to these and other ecosystem services, prairie dogs are considered ecosystem engineers and keystone species (Kotliar et al. 2006). Prairie dogs are also foundation species (Dayton 1972) that, by their historical abundance (Proctor et al. 2006), defined much of the structure of grassland communities and, in doing so, created suitable conditions for other species.

Y. pestis was first detected in prairie dogs during the 1930s (Eskey & Haas 1940). In an area of a plague epizootic, 95–100% of prairie dogs die (Cully et al. 2006), and plague-caused mortality persists to some degree between outbreaks (Biggins et al. 2010). Currently, *Cynomys* species are restricted to <5% of their historic areas of occupancy, plague is entrenched in most populations, and the disease is spreading to more eastern colonies (Proctor et al. 2006; Cully et al. 2010).

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It has long been recognized that plague poses a direct, serious challenge to conservation of prairie dogs (Torres 1973). Four U.S. species of prairie dogs that inhabit northern mixed grass prairie, shrub grassland, southern mixed grass prairie, shortgrass prairie, and intermountain grasslands in 11 U. S. states provide examples of the challenge. These examples demonstrate that plague can dramatically reduce the abundance of prairie dogs throughout large expanses of land, induce oscillations in prairie dog densities, restrict prairie dogs to chronically low densities, and rapidly accelerate the rate of colony turnover and movement (Supporting Information).

These direct effects of plague on prairie dogs have been emphasized historically, providing a rich collection of literature on the topic. In contrast, researchers have rarely evaluated the indirect effects of plague on grassland ecosystems (Biggins & Kosoy 2001*b*; Antolin et al. 2002). We believe that considering plague within the transformer species concept will provide a framework that formalizes and energizes discussion of the indirect effects of plague on grasslands.

Accumulating evidence demonstrates that the loss of prairie dogs to *Y. pestis* indirectly changes the character, condition, form, or nature of grassland ecosystems, a prerequisite for classification as a transformer species. In particular, plague transforms these ecosystems by causing "structural or compositional modifications, alterations in the import or export of nutrients, loss of resilience to disturbance," and decreases in native species abundance and diversity (Soulé et al. 2003:1239).

Effects of Prairie Dog Grazing and Clipping on Plant Communities

Black-tailed prairie dogs (*C. ludovicianus*) graze in ways that reduce the height of vegetation and facilitate an abundance of forbs and genetically distinct and relatively prostrate grasses (Detling 2006). Vegetative communities change when prairie dogs are removed. In Wind Cave National Park, South Dakota, active exclusion of black-tailed prairie dogs from a colony, which simulated a plague epizootic, resulted in an approximate 35% increase in plant biomass, reduced forb abundance, and a concomitant increase in the abundance of tall graminoids (Cid et al. 1991). Four years after prairie dogs were poisoned in areas of the Conata Basin, South Dakota, biomass of buffalo grass (*Bouteloua dactyloides*) increased by about 83% (Uresk 1985). During another study in Conata Basin, the U.S. Forest Service detected a >2-fold increase in vegetation height in an area where prairie dogs were removed via poisoning 2 years earlier (Griebel 2009). In Colorado, scarlet globe mallow (*Sphaeralcea coccinea*) (a forb) declined dramatically on colonies extirpated by plague and grasses increased in abundance (Hartley et al. 2009). In the same area of Colorado on sites occupied by black-tailed prairie dogs for 1–4 years but currently unoccupied due to recent plague epizootics, plant cover and composition transformed to conditions similar to unoccupied sites (more grasses) within a single growing season (Augustine et al. 2014).

Shrubs and woody plants continue to encroach on the grasslands of western North America (Van Auken 2000), in some areas because black-tailed prairie dogs are increasingly rare. During an experiment in Texas, *Prosopis* mesquite trees were planted in areas occupied by black-tailed prairie dogs. The prairie dogs removed all the mesquite within just 2 days (Weltzin et al. 1997). At the same site, 23 years after the removal of prairie dogs by poisoning, *Prosopis* had spread to 61% of ground cover (Weltzin et al. 1997). Similarly, when black-tailed prairie dogs were poisoned at the boundaries of a colony in Chihuahua, Mexico, mesquite became established 1450 m into the poisoned area, a 43% advance (List 1997; Ceballos et al. 2010).

Y. pestis can also facilitate the expansion of Russian thistle (*Kali tragus*), an annual forb that was introduced to North America in the late 1800s. In the Janos-Casas Grandes region of northwestern Chihuahua, Mexico, biologists removed black-tailed prairie dogs from treatment sites, but prairie dogs were left in other control sites (Davidson et al. 2010). About 1.5 years later, Russian thistle was 2 times taller and observably more abundant in the treatment plots.

Prairie dogs also influence the nitrogen content and digestibility of vegetation (Detling 2006). Over a single growing season in South Dakota, nitrogen concentration and digestability of graminoids were about 10% greater on a black-tailed prairie dog colony than an off-colony site (Coppock et al. 1983). The nitrogen concentration of forbs was about 40% greater on old colonies, suggesting a long-term benefit of prairie dog occupancy (Coppock et al. 1983). During another study in South Dakota, the nitrogen concentration of grasses and forbs was about 10-30% greater, and net mineralization of nitrogen was greater on colonies (Fahnestock & Detling 2002). The nitrogen content of plants declines when prairie dogs are removed or excluded from areas (Cid et al. 1991). This ecosystem change could affect the attractiveness of prairie dog colonies to at least some ungulates (Whicker & Detling 1988).

The Mountain Plover (*Charadrius montanus*), a ground-nesting bird of conservation concern (Dinsmore et al. 2005), benefits from vegetative alterations caused by prairie dogs. These plovers commonly nest on colonies of black-tailed and Mexican prairie dogs (*C. mexicanus*), where vegetation is short and patches of bare ground are common (Knowles et al. 1982). Plover numbers decline, sometimes dramatically, when plague erupts in prairie dogs (Dinsmore et al. 2001; Augustine et al. 2008; Dinsmore & Smith 2010).

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Effects of Prairie Dog Burrowing on Soils and Physical Characteristics of Colonies

Prairie dogs can remove about 225 kg of soil when creating a burrow system (Munn 1993), and the densities of their burrow openings can be 20–40/ha in some areas. These numbers translate into the movement of about 4500–9000 kg of soil/ha, which demonstrates that prairie dogs contribute greatly to soil turnover in grasslands (Whicker & Detling 1988).

The burrowing activities of prairie dogs "change soil chemistry, increase microporosity of soil to allow deep penetration of precipitation, and increase the incorporation of organic materials into the soil" (Miller et al. 2000:320). In the grasslands of northwestern Chihuahua, Mexico, soils hardened, water infiltration was reduced by 21%, and soil carbon storage was reduced by 54% when black-tailed prairie dogs were removed (Martínez-Estévez et al. 2013).

The construction of burrows adds an important structural feature to prairie grasslands. These burrows provide escape cover, shelter from inclement weather, nesting habitat, and foraging habitat for numerous vertebrate and invertebrate species (Slobodchikoff et al. 2009). Burrows collapsed only 3 years after prairie dogs were removed from colonies in Oklahoma (Butts & Lewis 1982). Wilcomb (1954) suggests burrows can collapse within 2 years of prairie dog removal.

The Western Burrowing Owl (*Athene cunicularia*) commonly inhabits colonies of prairie dogs, where they usurp burrows as nesting sites. Predator detection is enhanced for burrowing owls because *Cynomys* emit alarm vocalizations when a predator is present, thereby alerting owls to predators (Bryan & Wunder 2013). Also, vegetation on black-tailed prairie dog colonies is short, creating open vistas (Butts & Lewis 1982). In Nebraska burrowing owl populations declined by 63% when humans poisoned colonies of black-tailed prairie dogs (Desmond et al. 2000). In 1998 surveys of burrowing owls on 14 national grasslands from Texas to North Dakota detected owls on 69% of active black-tailed prairie dog colonies, but owls were detected on only 11% of colonies affected by plague epizootics (Sidle et al. 2001). In Colorado burrowing owls were nearly absent in black-tailed prairie dog colonies that had been extirpated by plague (Conrey 2010). This effect of plague is especially germane to conservation because the Western Burrowing Owl is a species of concern in the United States, Canada, and Mexico (Sheffield 1997).

Prairie dogs affect the structure of arthropod communities via their effects on vegetation, soils, and physical structures such as mounds and tunnels (Bangert & Slobodchikoff 2006). Various arthropods are attracted to prairie dog colonies, including anthophilous insects that visit flowering forbs, for instance, as found in colonies of black-tailed prairie dogs in northeastern Colorado (Hardwicke 2006). Some of these insects use loose soils around burrow mounds to create nests (Hardwicke 2006). Plague alters arthropod communities in grasslands via its direct effects on prairie dogs and indirect effects on vegetation and soils (Bangert & Slobodchikoff 2006; Hardwicke 2006). Moreover, by affecting anthophilous insects, plague may indirectly affect flowering plants that rely on arthropod pollinators for dispersal and fertilization (Hardwicke 2006).

Prairie Dogs as Prey

The historic abundance of prairie dogs contributed to their classification as a foundation species. Prairie dog colonies are favored hunting areas for multiple species of raptors and mammalian predators. The abundance of Ferruginous Hawks (*Buteo regalis*), a species of conservation concern, commonly decreases when plague erupts into epizootic form. Females produce 1 brood per year, and the number of chicks per brood is closely related to the abundance of food (U.S. Fish and Wildlife Service 1996). In 2 sections of Moreno Valley, New Mexico, Ferruginous Hawks declined in number by >75% after a plague epizootic in the local population of Gunnison's prairie dogs (*C. gunnisoni*) (Cully 1991). In a separate study in Colorado, a population of Ferruginous Hawks declined by about 89% subsequent to a plague epizootic in black-tailed prairie dogs during 1988–1989; increased as the prairie dog population recovered; and declined by about 63% subsequent to another epizootic during 1994–1995 (Seery & Matiatos 2000; see also Plumpton & Andersen 1998).

Black-footed ferrets (*Mustela nigripes*) are endangered carnivores that selectively prey on prairie dogs and use prairie dog burrows as den sites (Miller et al. 1996). Ferrets are indirectly and directly affected by plague. Indirectly, ferrets are affected when plague substantially reduces a prairie dog population because less food and fewer burrows are available. Directly, ferrets are highly susceptible to plague infection and mortality. In a complex of white-tailed prairie dog (*C. leucurus*) colonies near Meeteetse, Wyoming, an epizootic of plague and canine distemper reduced the abundance of ferrets from 129 in fall 1984 to 16 in fall 1985, and the free-ranging population was ultimately extirpated (though some ferrets were captured to initiate a captive breeding program) (Forrest et al. 1988). At the Conata Basin, South Dakota, plague reduced a population of ferrets from 335 in 2007 to 32 in 2013 (T.M. Livieri, Prairie Wildlife Research). In Montana enzootic plague (between epizootics) reduced ferret survival by 240% (Matchett et al. 2010).

Looking Ahead

Our nonexhaustive search of the literature demonstrated that *Y. pestis* affects the nature of grasslands over a

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substantial area and causes changes in the structure or function of ecosystems, requisites for classification as a transformer species (Richardson et al. 2000). In a recent treatise on transformer species, Ehrenfeld (2011:668) noted that "While there are no generally accepted quantitative criteria for determining when a change in structure or function is 'substantial', the concept implies that more than one, and usually several, of the components of an ecosystem, such as species abundances, nutrient flux rates or pool sizes, food web connections, or physical structure, are significantly altered by the presence of the transforming species." We found that, by reducing densities and distribution of prairie dogs in the grasslands of western North America, *Y. pestis* can cause declines in native species abundance (mortality) and diversity (extirpations), including threatened and endangered species; alterations in food web connections; alterations in the import or export of nutrients; loss of resilience to encroaching woody plants; and modifications of physical structures such as burrows. Thus, we conclude that *Y. pestis* is a transformer species in the grasslands of western North America.

The plague bacterium was introduced to North America about 114 years ago, and the array of implications of this introduction for wildlife is not yet fully understood (Biggins & Kosoy 2001*a*). We believe we have shown that *Y. pestis* is transforming grassland ecosystems in western North America. However, the ecological implications of plague extend beyond grasslands.

Y. pestis has been detected in various ecoregions inside 17 western U.S. states, including marine west coast forests, northwestern forested mountains, North American deserts (except the hottest and driest areas), Mediterranean California, southern semiarid highlands, and the Great Plains (Commission for Environmental Cooperation 1997). In these ecoregions, pathogenic effects of plague have been noted in mice, voles, rats, squirrels, marmots, and prairie dogs (Perry & Fetherston 1997), and over half the rodent species of conservation concern in the United States occur within the range of plague (Hafner et al. 1998). Lagomorphs are also infected under natural conditions, and infections have been noted in various Carnivora, including canids, felids, and mustelids (Salkeld & Stapp 2006). Furthermore, >230 North American flea species are infected with *Y. pestis* in the wild (Eisen et al. 2009).

The widespread distribution of plague at multiple trophic levels in North America and its lethality in various mammals suggest the disease may be affecting ecological relationships throughout the western half of the United States. Thus, research should seek to acquire a more complete understanding of the disease's effects on ecosystems and develop tools for its control. In particular, the following topics are in need of urgent attention from conservation scientists.

First, little is known about how *Y. pestis* persists during enzootic periods. The disease is maintained in host and flea populations between epizootic outbreaks (Matchett et al. 2010) but the mechanisms of persistence remain elusive. Various hypotheses deserve investigation (reviews in Eisen & Gage 2009; Wimsatt & Biggins 2009; Gage 2012).

Second, there is an acute need to rapidly expand data collection across host species to better understand the effects of enzootic plague. We suspect that plague is affecting host populations by dramatically increasing oscillations in abundance while chronically dampening the mean densities of small mammals, thereby reducing prey biomass and altering competitive relationships. Although major epizootic events are obvious for some species, much of the effect of plague is insidious and difficult to detect without intensive studies (Biggins et al. 2010; Matchett et al. 2010).

Third, studies are needed to investigate the efficacy of the tools used to manage plague. Research is underway with prairie dogs to evaluate a recently developed bait-delivered vaccine that can be distributed across vast landscapes (Abbott et al. 2012). Research is needed to develop other mitigation tools. An integrated approach to management would include a variety of tools coupled with prescriptions of when and where various methods can be most efficiently applied. The latter requires a better understanding of plague ecology.

Fourth, research is needed to evaluate how weather affects plague so future scenarios can be considered under projections of climate change and interventions can be most efficiently applied. The best approach may be to evaluate the effects of temperature, humidity, and precipitation on fleas, *Y. pestis*, and mammals at various ecological scales (Ben-Ari et al. 2011; Eisen & Gage 2012). We suggest increased use of controlled experiments rather than undue reliance on conceptual and mathematical models.

Overall, much of the grassland ecosystems in North America may be disrupted. Because of the early invasion of *Y. pestis* in the western United States, there is a strong possibility that shifting baselines may be distorting definitions of functional grassland ecosystems in the region (McDonald et al. 2011). There is a relatively large amount of supporting data for the concept of *Y. pestis* as a transformer species in the prairie dog system, but the organism simply has not been studied in this context in enough areas of western North America to identify the scope of its transforming influence in other systems. In South America and other parts of the world, the ecological transformations conceivably mediated by introduced plague have received even less attention. It seems judicious to heed the warning flag raised by the effects of plague on prairie dogs, endangered black-footed ferrets, and the structure and function of grassland ecosystems in

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western North America. The future of prairie dogs and ferrets, and perhaps other animals in the range of introduced *Y. pestis*, relies heavily on the ability to manage plague.

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Supporting Information

Examples of the direct effects of *Y. pestis* on prairie dog populations are available as part of the on-line article (Appendix S1). The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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