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Review

Local Scale Effects of Disease on Biodiversity

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Abstract: To date, ecologists and conservation biologists have focused much of their attention on the population and ecosystem effects of disease at regional scales and the role that diseases play in global species extinction. Far less research has been dedicated to identifying the effects that diseases can have on local scale species assemblages. We examined the role of infectious disease in structuring local biodiversity. Our intention was to illustrate how variable outcomes can occur by focusing on three case studies: the influence of chestnut blight on forest communities dominated by chestnut trees, the influence of red-spot disease on urchin barrens and kelp forests, and the influence of sylvatic plague on grassland communities inhabited by prairie dogs. Our findings reveal that at local scales infectious disease seems to play an important, though unpredictable, role in structuring species diversity. Through our case studies, we have shown that diseases can cause drastic population declines or local extirpations in keystone species, ecosystem engineers, and otherwise abundant species. These changes in local diversity may be very important, particularly when considered alongside potentially corresponding changes in community structure and function, and we believe that future efforts to understand the importance of disease to species diversity should have an increased focus on these local scales.

Key words: disease, biodiversity, population, community, local scale

INTRODUCTION

Infectious diseases in wildlife are emerging at unusually high rates around the world, raising concern that they may pose a substantial threat to biodiversity (Harvell et al., 2002; Wilcove et al., 1998; Jones et al., 2007). Infectious diseases have the potential to play a significant role in regulating the composition, diversity, and richness of species found within communities, and ultimately to affect global levels of biological diversity. This may occur because diseases are able to facilitate declines in local populations, the contraction of geographic ranges, and can evolve to infect numerous hosts (Daszak et al., 1999, 2001; Estes et al., 2003; Walsh et al., 2003).

At the global scale, infectious disease is not considered a significant driver of species extinction relative to other forces, such as habitat loss and overexploitation (Smith et al., 2006, 2009; Pedersen et al., 2007). This is largely due to a paucity of historical records and uncertainty in available data that make it difficult to fully understand the role infectious diseases play in species extinction (Smith et al., 2006, 2009; Pedersen et al., 2007). However, the study of infectious disease has a solid foundation in epidemiology and mathematical modeling (Anderson and May, 1992),

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which suggests that disease-mediated extinction is indeed rare. Theory predicts that infectious agents should only drive species to extinction under specific circumstances: when pre-epidemic population size is small, when reservoir hosts are available, when the infectious agent can survive in the abiotic environment, or when transmission is a function of the frequency of infected individuals and not subject to population density thresholds (i.e., sexually transmitted diseases) (Thrall et al., 1993; De Castro and Bolker, 2005; Fenton and Pedersen, 2005; Pedersen et al., 2007). To date, ecologists and conservation biologists have focused much of their attention on the population and ecosystem effects of disease at regional scales, and the role that diseases play in global species extinction (Smith et al., 2006, 2009; Pedersen et al., 2007). Far less experimental work has been dedicated to identifying local impacts of disease on community structure and biodiversity. We have considered the role of infectious disease at the local scale and present three new case studies that help to illustrate the range of impacts that infectious diseases can have on community structure and biodiversity.

LOCAL SCALE EFFECTS OF INFECTIOUS DISEASE

At local scales, infectious disease may cause or facilitate numerous changes in the structure of species assemblages (Hudson et al., 2002). After the emergence of the myxoma virus into England, for example, there was a rapid decline in rabbit (*Oryctologus cuniculus*) populations, which altered vegetation patterns and both invertebrate and vertebrate communities (Minchella and Scott, 1991). Similarly, the arrival of Dutch elm disease in England had various consequences for plant and animal communities. While the availability of forest habitat for many bird species declined, an increase in beetle larvae in dead trees resulted in increased food availability for others (Osborne, 1985). In 1889, the Italian army imported cattle that were carrying rinderpest virus (a Morbillivirus related to measles) from India to the Horn of Africa. Within a year, the virus spread to numerous species and caused mass mortality in domestic and wild artiodactyls populations (Plowright, 1982; Spinage, 2003). After 1961, when clinical rinderpest was eradicated, wildlife populations experienced rapid recovery and had corresponding effects on population dynamics and community structure (Sinclair, 1979; Plowright, 1982; Dobson, 1995; Tompkins et al., 2000). Increases in the abundance of ungulate species following rinderpest control led to an increase in the density of carnivores, particularly lions (*Panthera leo*) and hyenas (*Crocuta crocuta*), which were matched by decreases in the abundance of gazelles, most likely due to increased predation pressure. Collectively, the regulatory effects and trophic cascades initiated by these events suggest that certain diseases can play keystone roles in ecosystem functioning and structure. With respect to species diversity, however, only three potential outcomes are conceivable when disease occurs in a local community of organisms.

First, a disease may have no significant effect on diversity. This can occur, for example, if a disease causes few species extirpations within a community, or if the species extirpations caused by a disease are largely matched by the compensatory establishment of other species. Second, a disease may cause or facilitate a decrease in species diversity. This can occur, for example, if a disease were to remove a keystone species or ecosystem engineer from an assemblage, causing a cascade of extirpation events, or more generally if species that are extirpated from an assemblage are not replaced by the compensatory establishment of other species. Third, a disease may cause or facilitate an increase in diversity. This can occur, for example, if a previously dominant species is reduced in abundance or extirpated from an assemblage, such that there is an increase in the quantity of limiting resources available; this might result in a more evenly distributed assemblage of species or an overall increase in the number of species present.

It is difficult to determine the relative frequency of these three possible responses (no change, an increase, or a decrease in diversity) given the shortage of scientific studies that explicitly examine the effects of disease on local scale biodiversity. Largely, this is due to a lack of long-term data on community assemblages before and after an infectious disease emerges (i.e., shifts its geographic range, evolves, infects new host species, or increases in incidence). This is an important topic to consider, however, as many scientists cite anecdotal evidence that recent disease epidemics significantly impact local species diversity. For example, researchers in Tasmania believe that the rapid loss of Tasmanian devils (*Sarcophilus harrisi*) to devil facial tumor disease is leading to population increases in two harmful invasive predators, feral cats and European red foxes (*Vulpes vulpes*), which they fear will threaten native species diversity just as they did in mainland Australia (Jones et al., 2007). Likewise, in Australia, the introduction of rabbit hemorrhagic disease as a biocontrol for the European rabbit (*Oryctolagus cuniculus*) seems to have facilitated population recovery among competing native granivorous rodents: Western grey and red kangaroos (respectively, *Macropus fuliginosus* and *Macropus rufus*) (Mutze et al., 2008). Similarly, the infectious fungus *Batrachochytrium dendrobatidis*, which causes the deadly disease chytridiomycosis in amphibians, may have significant effects on local species communities. As evidenced by *B. dendrobatidis* epidemics in amphibian communities around the world, catastrophic declines and recent species extinctions associated with disease are more than a theoretical possibility (Collins and Storfer, 2003). The loss of so many individual amphibians to *B. dendrobatidis*, and the recent irreversible loss of several species to the disease, is believed to alter aquatic and terrestrial food webs, nutrient cycling, algal biomass, and insect abundance. Unfortunately, scientists have been unable to study the local scale effects of amphibian declines after epidemics of *B. dendrobatidis.*

Evaluating the impact of disease on local biodiversity is tricky, but we can begin to gain some understanding of the issue by considering disease emergence in local communities. Emerging infectious diseases are defined as those caused by parasites and pathogens that have recently increased in incidence, occupied host species or geographic extent, have been newly discovered, or are caused by a newly evolved agent (Lederberg et al., 1992). By altering the abundance and distribution of particular species, emerging diseases can cause large changes in community structure that lead to increases, decreases, or relatively little change in diversity. Our intention here is to illustrate how these variable outcomes can occur by focusing on three local scale case studies of disease emergence: the influence of chestnut blight on forest communities dominated by chestnut trees, the influence of red-spot disease on urchin barrens and kelp forests, and the influence of sylvatic plague on grassland communities inhabited by prairie dogs. The differential impact of diseases on these communities suggests that the role of disease, while often being extremely important, is highly variable, and is not a consistent a threat to local species diversity. Although important, it is outside the scope of this review to consider the relative effects of disease compared with other environmental forces (i.e., climate change, habitat loss, overexploitation) on local diversity (see Smith et al., 2009). Likewise, whereas analogies have been drawn between emerging diseases and invasive species, we do not address this topic.

CHESTNUT BLIGHT IN NORTH AMERICA

Before the establishment of chestnut blight (*Cryphonectria parasitica*) in eastern North America, the American chestnut (*Castanea dentata*) was an important canopy component of eastern deciduous forests. In local areas the American chestnut often formed up to 90 percent of the total wood volume (Korstian and Stickel, 1927) and over broader areas of its geographic range it probably composed more than 40 percent of the total number of canopy trees (Keever, 1953). This relatively high level of abundance and dominance was dramatically changed by the chestnut blight, which was introduced to North America through the horticultural trade and was first discovered in New York City in 1904 (Keever, 1953). In less than 50 years blight spread throughout the natural range of the American chestnut, from northern New England to the southern Appalachians, causing a transformation in the American chestnut from an abundant overstory tree to an occasional understory shrub (Paillet, 2002). Although chestnuts are clearly persisting (through clonal growth), their former role as a dominant member of many eastern forest communities has been dramatically changed. This disease-induced change in the functional role of the American chestnut consequently has had tremendous impacts on the structure of tree communities throughout its geographic range, where other tree species have become dominant in their absence (Korstian and Stickel, 1927; Keever, 1953; Nelson, 1955; McCormick and Platt, 1980). We are concerned with the role that these disease-induced changes may have had on species diversity at local spatial scales, i.e., within species communities.

Few data sets exist that compare tree species diversity at particular sites before and after chestnut blight reached an area. Nonetheless, two such studies exist and from these we can draw some inferences about the types of changes that occurred. At the Coweeta Hydrologic Laboratory in eastern North Carolina, the effects of chestnut blight on tree communities were recorded in 1934 shortly after blight reached the area, in 1941 after the blight began to induce chestnut mortality, and again in 1953 after chestnuts were largely replaced as canopy trees (Nelson, 1955). Across this time interval, as chestnut abundance declined, tree species that were abundant showed progressive increases in species evenness; this is shown graphically as a progressive flattening of their rank-abundance distributions (Fig. 1a). Rare species, which were lumped together as a single group by

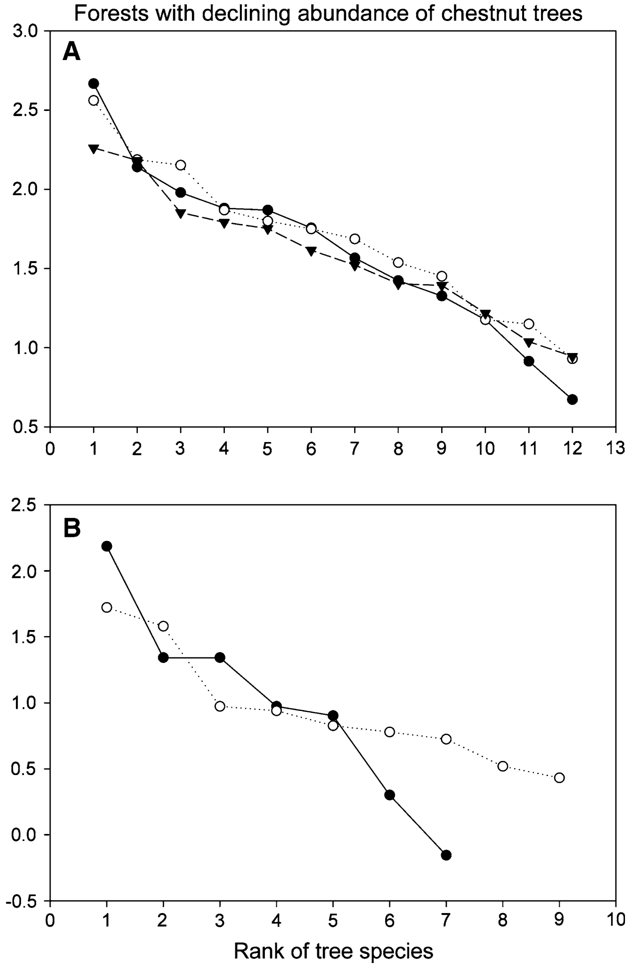

Figure 1. The impacts of declining American chestnut abundance on tree communities. Abundance was measured as the log number of stems per acre. **a** Change in relative abundance of the most common canopy trees in a North Carolina forest in 1934 (*closed circles*), 1941 (*open circles*), and 1953 (*triangles*) as chestnut trees declined from the most to least abundant species. Note that in addition to a decline in the dominance of any single tree species (and to a corresponding increase in species evenness) that four additional tree species (not shown on this figure) invaded after a decline in chestnut tree abundance, such that the net diversity of tree species increased (Nelson, 1955). **b** Change in relative abundance of canopy trees in Connecticut forests surveyed before (*closed circles*) and after (*open circles*) the removal of chestnut trees, which were the most abundant species initially, and completely absent after their removal; this lead to an increased evenness and richness (and hence diversity) of canopy tree species (Korstian and Stickel, 1927)

Nelson (1955), behaved consistently with more abundant species by also showing increased abundance after chestnut declines. In addition to the increases in evenness (and hence diversity) that are shown in Fig. 1a, Nelson (1955) also documented increases in the total number of tree species occupying areas formerly dominated by chestnuts, where several additional tree species invaded—further increasing species richness and diversity. Similar changes were observed in a study by Korstian and Stickel (1927), who examined forests in Connecticut that were surveyed before and after chestnut trees had been "salvaged," i.e., removed, in anticipation of the coming blight. Taking an average across several forest plots they documented an increase in species evenness and richness (and therefore in diversity) of canopy trees after the removal of chestnuts; this is shown graphically as a decrease in the slope and an increase in the length of the subsequent rank-abundance curve (Fig. 1b). It is unclear, however, whether these increases in richness are simply due to the emergence of subordinate trees into the canopy or due to the addition of species to the community. Nevertheless, the combined results of these studies provide convincing evidence that at a minimum, species evenness increased after the demise of chestnut trees, facilitating an increase in local species diversity.

Although the evidence for increasing tree diversity after the removal of chestnut trees is strong, these data do not demonstrate how other associated components of these species assemblages might have changed. On the one hand, given the known allelopathic impacts of American chestnut litter (Vandermast et al., 2002), we might expect that the diversity of understory vegetation also increased after declines in chestnut abundance; however, evidence to support this conjecture is unavailable. On the other hand, given the loss of chestnut seed production (Paillet, 2002), we might expect that diversity of granivorous species decreased locally; this assumes, however, that compensatory increases in oak species abundance, and hence acorn production, in these systems (Nelson, 1955) has not mitigated the loss of chestnut seeds. Still, it seems likely that at least some species could have been negatively impacted by the decline in chestnut tree abundance, which in turn could have caused the loss of some species locally. However, we do not know whether other species were able to be added locally, due to the corresponding increase in other resources. Therefore, with the data available, it seems uncertain how elements of forest species assemblages (other than the trees themselves) might have changed in diversity at local scales after the decline in chestnut abundance.

RED-SPOT DISEASE: SEA URCHIN BARREN AND KELP FOREST DYNAMICS

At temperate latitudes on the west coast of North America, kelp "forests" form one of the most distinctive subtidal habitats in the world (Steneck et al., 2002). These habitats are structured predominately by *Macrocystis pyrifera*; a brown algal species that can grow to more than 40 m in height, extending from subtidal rocky or sandy substrates to surface waters (Foster and Schiel, 1985). The extensive three-dimensional distribution of *M. pyrifera* creates a heterogeneous habitat and supplies energy that supports a diverse assemblage of vertebrate, invertebrate, and algal species, which together comprise the kelp forest communities of the Northeast Pacific. *Macrocystis* kelp forests are dynamic communities that are subject to periodic eradication by factors, including extreme storm events and population outbreaks of sea urchins. Sea urchins feed extensively on the algae that maintain *Macrocystis* kelp forests (Ebeling et al., 1985). At high urchin densities, this can cause dramatic declines in *M. pyrifera* and replacement of kelp forest communities with urchin barrens (Tegner and Dayton, 2000).

Historically, the role of sea urchins in the local destruction of Northeast Pacific kelp forests was mediated by predators, such as sea otters (*Enhydra lutris*). A primary predator of urchins, sea otters can dramatically reduce urchin abundance, thereby releasing kelp forests from regulation by urchin herbivory (Estes and Palmisano, 1974). Today, in the absence of sea otters from the majority of their historic range, as well as the absence or reduced abundance of other historic urchin predators, periodic urchin population explosions lead to the regular removal of kelp forest habitats (Estes et al., 2003). However, in the last two decades another "predator," red-spot disease, has altered local populations of sea urchins in the waters of coastal California (Behrens and Lafferty, 2004; Lafferty, 2004; Lester et al., 2007). Epidemics of red-spot disease have repeatedly decimated local urchin populations (e.g., purple and red sea urchin *Strongylocentrotus purpuratus* and *S. franciscanus*) that reach high densities (Behrens and Lafferty, 2004; Lafferty, 2004).

Red-spot disease now seems to play a dominant role in reducing abundance of urchins, thereby facilitating the recovery of kelp forest communities (Lafferty, 2004). It is not clear, however, whether restoration of kelp-forests will necessarily lead to significant changes in the associated species diversity of these communities. It often is assumed that urchin barrens are species poor habitats, but this is not necessarily true, and many urchin barrens actually support relatively species rich communities (Graham, 2004). However, even if species-rich communities persist, the removal of kelp forests may still lead to large declines in the species diversity in certain functional groups (e.g., 40% decline in sessile invertebrate diversity) (Graham, 2004).

We provide an example of how the red-spot disease has mediated community structure at a site in the California Channel Islands, where the habitat has been transformed from an urchin barren to a kelp forest (Behrens and Lafferty, 2004). At this site in 1992, an urchin barren was struck by an epidemic of red-spot disease, releasing kelp from strong herbivory pressure and allowing this habitat to revert back to a kelp forest by the following year, in which state it remained until 1996 (Table 1). After the transition from urchin barren to kelp forest, and during the next several years, there was relatively little change in the richness of taxa present at the site (Table 1). This suggests that disease, at least at this site, despite playing a large role in determining habitat structure, has played a negligible role in affecting species richness.

There are four principal reasons why we may not have found evidence for a positive effect of red-spot disease on diversity in these systems, despite the keystone role it plays in reducing herbivore pressure and allowing the restoration of kelp-forest communities. First, species richness per se was not sampled at these sites. Many of the species in these communities form taxonomically complex groups that are difficult to distinguish in most subtidal sampling regimes. As a consequence, richness of taxa was sampled with the implicit

Table 1. Red Spot Prevalence and Community Change at Cat Canyon, Santa Barbara Island, California Channel Islands in the 1990s[a]

Year	Prevalence[b]	Community type	Taxonomic richness
1992	4	Urchin Barren	41
1993	2	Kelp Forest	36
1994	0	Kelp Forest	38
1995	0	Kelp Forest	42
1996	0	Kelp Forest	37

[a] Data from Richards and Kushner (1994); Kushner et al. (1995a, b, 1997a, b)

[b] Prevalence of red spot disease in *S. purpuratus* and *S. franciscanus* categorized as: 0 = 0%, 1 = <5%, 2 = 5–25%, 3 = 25–75%, 4 = >75%

understanding that the number of taxa recorded underestimates the number of species present. Second, the richness of species at local sites in these systems may have been reduced by long-term fluctuations between urchin barrens and kelp forests that have extirpated species not able to persist in both habitat types. Third, given the likely persistence of specialist species across the mosaic of habitats in this region, it is conceivable that time lags in the colonization of individual sites may temporarily reduce species richness after the conversion of an urchin barren to a kelp forest habitat. Fourth, evidence of a change in species richness may not have been detected because it simply did not occur. Although conversion of an area from one habitat type to another is expected to lead to large changes in diversity, it has been shown in a diversity of circumstances that this is not always the case (e.g., Brown et al., 2001; Sax, 2002). In fact, oftentimes communities dominated by completely different species retain almost precisely the same number of species (Sax et al., 2005). Consequently, it is conceivable that red-spot disease, despite the changes it mediated in community structure from an urchin barren to a kelp forest, has not lead to a change in species richness at local scales.

SYLVATIC PLAGUE IN NORTH AMERICAN PRAIRIE DOGS

Historical records suggest that prairie dogs (genus *Cynomys*) may have been the most abundant herbivorous mammal in North America at the time of the first Euro-American explorations of the West (Seton, 1929; Cully, 1989), having enormous effects on the structure of local communities (Detling and Whicker, 1988; Reading et al., 1989). Through their burrowing and grazing activities, prairie dogs are ecosystem engineers. Their preferential feeding behaviors altered plant species composition, abundance, and diversity (Coppock et al., 1983; Weltzin et al., 1997), their creation of burrows and a heterogeneous landscape of patchy vegetation provided habitat for numerous grassland species, and their abundance, distribution, and size made them optimal prey for a variety of predators (Clark et al., 1982; Kotliar et al., 1999). Today their influence is greatly diminished because all five species have suffered drastic declines in population abundance and distribution during the past 100 years. These declines in prairie dog abundance are largely attributable to three major factors: rodent poisoning programs, habitat loss, and sylvatic plague (Cully, 1989; Knowles and Knowles, 1994). The impact of these declines has been well-studied among three prairie dog species: black-tailed (*Cynomys ludovicianus*), Gunnison's (*C. Gunnisoni*), and white-tailed (*C. leucurus*). All three species are highly susceptible to sylvatic plague, to which they have little or no immunity, with resulting population mortality inevitably in excess of 99.5% (Clark, 1989; Cully, 1989; Cully et al., 1997). Consequently, the removal of prairie dogs provides us with an opportunity to understand how disease (sylvatic plague) can impact species diversity at local scales.

We can estimate the importance of sylvatic plague by examining the results of experimental studies and surveys that explore the impacts of prairie dog removal on subsequent characteristics of grassland assemblages. In particular, we can examine four types of evidence: prairie dog exclusion studies, colony vs. adjacent non-colony comparisons, active vs. abandoned colony comparisons, and post-eradication surveys. Collectively, these studies suggest that prairie dog removal can have a significant effect on the diversity of faunal and floral species. Numerous studies have shown that prairie dog ecosystems support a greater diversity of small mammals, terrestrial predators, and avian species than undisturbed grasslands (see Kotliar et al., 1999 for a complete review). The principal explanation for these declines in diversity across animal taxa seems to be the loss of burrowing habitat, and overall heterogeneity, provided by prairie dogs (Kotliar et al., 1999). The local effects of prairie dog removal have scaled up to cause the near extinction of black-footed ferrets (*Mustela nigripes*) and the proposal of ferruginous hawks (*Buteo regalis*), mountain plovers (*Charadrius montanus*), burrowing owls (*Athene cunicularia*), and swift foxes (*Vulpes velox*) as candidate species under the Endangered Species Act (Miller et al., 1994). With respect to plant species, the effects of prairie dog removal are less straightforward. Several studies on black-tailed prairie dogs suggest a greater diversity of plant species within prairie dog habitats; two studies on Gunnison's prairie dogs describe lower diversity of plant species within prairie dog habitats, and two reviews on the effects of white-tailed prairie dogs report no difference in diversity of plant species within prairie dog habitats (Table 2). The inconsistency between studies on different prairie dog species suggests that the impact of their removal on plant diversity at local scales is dependent on the particular prairie dog species that is removed.

Overall, this evidence suggests that the extirpation of prairie dog populations by sylvatic plague should have significant effects on diversity of both plant and animal

Table 2. Floral Species Composition and Diversity in the Presence and Absence of Three Prairie Dog Species

Species	Study type	Dominant floral group		Highest diversity	Reference
		Prairie dogs	No prairie dogs		
Black-tailed	Pre/post abandonment[a]	Forbs	Graminoids	Pre-abandonment	Osborn and Allan (1949)
Black-tailed	Pre/post colonization[a]	Forbs	Graminoids	Post-colonization	Archer et al. (1987)
Black-tailed	Pre/post exclusion[a]	Forbs	Graminoids	No change	Cid et al. (1991)
Black-tailed	Colony vs adjacent area	Forbs	Graminoids	Colony	Bonham and Lerwick (1976)
Gunnison's	Pre/post reintroduction[a]	Graminoids	Graminoids	No change	Davidson et al. (1999)
Gunnison's	Pre/post colonization[a]	Graminoids	Graminoids	Pre-colonization	Slobodchikoff et al. (1988)
White-tailed	Review	Varied with study		No change	Tileston and Lechleitner (1966)
White-tailed	Review	Varied with study		No change	Hoogland (1981)

[a] Studies were conducted at least 1 year after the change in prairie dog presence

species at local scales. Vertebrate and invertebrate diversity should decline after prairie dog removal, whereas plant species diversity should increase, decrease, or remain unchanged depending on which prairie dog species is removed. Two points of caution should be considered when interpreting this evidence. First, given the limited number of studies available, we cannot rule out the possibility that the species-dependent results exhibited by plant diversity also may be site-dependent. Second, the results of the studies and surveys examined here were performed over relatively short periods of time, and it is conceivable that studies or surveys conducted during the course of many years (or even centuries) would result in different conclusions. Nevertheless, we are confident that at least over the short-term, sylvatic plague plays a strong role in mediating local levels of species diversity in grassland communities dominated by prairie dog colonies.

CONCLUSIONS

At local scales infectious disease seems to play an important, although difficult to predict, role in structuring species diversity. As we have shown, diseases can cause drastic population declines or local extirpations in keystone species, ecosystem engineers, and otherwise abundant species. By reducing the abundance of these species, diseases can have highly variable effects on local diversity. Although we did not provide examples, disease also could conceivably alter local diversity by causing extirpations or declines in the abundance of rare species. Regardless of the mechanism, however, disease can have one of three effects on local diversity; it can cause diversity to increase, decrease, or remain relatively unchanged. These different impacts may be very important, particularly when considered alongside potentially corresponding changes in community structure and function, and we believe that future efforts to understand the importance of disease in mediating species diversity should explicitly consider changes at local scales.

During the long-term, we cannot rule out the possibility that disease will play a larger role in future species extinctions. At a global scale this is appears to occur most frequently when diseases interact synergistically with anthropogenic changes in the environment to cause declines in species abundance across their ranges (Smith et al., 2006, 2009). At local scales, synergistic interactions between disease and anthropogenic stressors may act to locally extirpate species. This could lead to cascades of events that continue to alter local diversity in ways that are difficult to generalize, i.e., to net increases, decreases, or lack of change in diversity depending on the particular communities affected. Only if these synergistic effects become exceedingly common would we expect to see general declines in local species diversity. So, although currently available evidence does not support the conclusion that infectious disease is a primary contributor to species extinctions at global scales, nor that disease should necessarily cause declines in diversity at local scales, we cannot rule out the possibility that these conditions could change. Future work can determine what the ultimate impacts of infectious disease will be on global levels of diversity and on the diversity of local communities. However, this will only be accomplished when conservation biologists, ecologists, and wildlife managers make the study and survey of infectious agents a regular component of their research programs.

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