As the Kangaroo Rat Goes, so Goes the Carrizo Plain

A little giant is the keystone species to a fragile ecosystem.

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The Carrizo Plain is caught in the middle. It's nestled in the Coast Range of California, halfway between San Francisco and Los Angeles, going north-south, and between San Luis Obispo and Bakersfield, going west-east. With its abundance of non-native grasses and very low precipitation, it's halfway between a desert and a grassland. Depending on which way you face, it's either one of the driest parts of coastal San Luis Obispo County or one of the wettest spots in Kern County. Despite the dry conditions, the alkaline Soda Lake fills up in most winters and provides valuable over-wintering habitat for cranes and other waterbirds.

In the mid-1940s, the Carrizo Plain served as a gunnery range. But in 1988, The Nature Conservancy (TNC), having encouraged farmers to donate land, formed a partnership with the U. S. Bureau of Land Management and the California Department of Fish and Game to protect as much as possible of "the largest, single native grassland remaining in California," according to TNC. In 2001, part of the southern half of the area was designated the Carrizo Plain National Monument. From an initial parcel of 82,000 acres, TNC and the two government agencies now manage approximately 250,000 acres. Despite its protected status, there are significant private in-holdings—the Carrizo Plain relies on private cattle grazing to maintain non-native plant cover—and the northern half hosts two of the largest solar energy installations in the world, and a burgeoning cannabis industry. Because of its incredible, endemic biodiversity—the Carrizo Plain area hosts the greatest concentration of threatened and endangered species anywhere in California—the Wilderness Society proposed that it be listed as a UNESCO World Heritage Site, but local governments successfully blocked the idea because the area is adjacent to some of the most productive oil fields in the country.

The Carrizo Plain is often referred to as "America's Serengeti." The Plain does host small herds of re-introduced tule elk, *Cervus canadensis nannodes*—a subspecies of elk found only in California—and pronghorn, *Antilocapra americana*. But they are not what makes the area unique. Chumash Indians, a group of tribes native to central coastal California, have a cosmology that recognizes three worlds: upper, middle, and lower. The upper world is dominated by the Sun and his fiery torch. The middle world is run by humans. And the lower world is inhabited by beings that emerge after the Sun goes to sleep, a panoply of animals that burrow to avoid the heat of the day. It's the lower world that generates so many species found nowhere else on Earth.

For decades, ecologists considered the Carrizo Plain—and

the great southern half of the Central Valley to the east—to be grassland. They reasoned that the region would have to be grassland to support the number of sheep and cattle that have been grazing there since the 1800s. The area looks like grassland—huge, flat expanses of golden grasses drying in the intense summer sun, occasionally interrupted by sparsely dotted ephedra, juniper, or atriplex, with curiously rounded hills in the distance. But looking more closely at the flora and fauna, and at the weather patterns, one realizes that the San Joaquin is also closely related to the desert. Recognizing the coexistence of these two environmental conditions matters because plants and animals have adapted differently to the harsh, variable climates of the desert than to the more temperate grasslands. Plants that might compete with each other, if given enough rain, suddenly become mutualists when confronted with the sere, dry soils of a desert. Conversely, grasses that respond well to grazing in the coastal fog belt might be out-competed by non-natives in the sun. Also, managing and conserving a desert ecosystem is very different from managing native perennial or annual grasslands.

The ecological history matters, too, because it can explain some of the unique evolutionary patterns found here. In the list of sensitive, threatened, and endangered species of the San Joaquin Valley—the San Joaquin kit fox, *Vulpes macrotis*, San Joaquin antelope squirrel, *Ammospermophilus nelsoni*, and blunt-nosed leopard lizard, *Gambelia sila*—all have close living relatives in the Mojave Desert, on the other side of the Tehachapi Mountains to the south. The San Joaquin Valley also inherited grassland species: some rare—the San Joaquin woolly thread, *Monolopia congdonii*—and some common—pronghorn and elk, badgers, and prairie falcons. And a suite of species cross the boundaries: ravens, badgers, whiptails, jackrabbits, rattlesnakes, and the occasional California condor.

One animal dominates the lower world of the Chumash: the giant kangaroo rat, *Dipodomys ingens*. At the center of this endangered ecosystem, the giant kangaroo rat, about the size of a medium baked potato, is endemic to the San Joaquin Valley. Other species of kangaroo rats are found throughout western North America and have adapted to arid and semi-arid grasslands and to deserts. They are all burrowers, dividing their lives between building and maintaining burrow systems and collecting and storing seeds in them. Although it's listed as Endangered by California and federal endangered species acts, the giant kangaroo rat can be found in breathtaking abundance in forgotten pockets of the San Joaquin Valley. They are not social animals, such as prairie dogs, but they tend to congregate in flat places, with loamy soils and the right balance of precipitation. If conditions are too dry, then not enough grasses grow to support their (relatively) large bodies. If too wet, grasses can grow too thick for them to move through with ease; seeds that they cache may mold; or they get out-competed by the much larger and more aggressive California ground squirrel, *Otospermophilus beecheyi*. Giant kangaroo rats are rarely found in areas that receive more than about thirteen inches of rain per year. They tend to rely on their neighbors for help avoiding predators, drumming their feet to warn of intruders. If you walk slowly through a giant kangaroo rat colony on a mid-summer night, you'll be serenaded by the rapid drumming of small, furred feet on lightly compacted soil.

With all species in a community dependent on one another—Muir's tangled web—understanding interactions is complicated, but we've gained good insight into giant kangaroo rat impact on the Carrizo because of a long-term ecological study established in 2007. In that experiment, wildlife ecologists Justin Brashares, at the University of California, Berkeley, and Laura Prugh, at the University of Washington, established thirty study plots, twenty of which have a rodent-proof fence built in the middle. Inspired by other valuable studies throughout the San Joaquin on the interactions between kangaroo rats and their community, these exclosures provide unique insight to what happens when the keystone giant kangaroo rat is removed from the system.

By excavating soil from within their burrows to the surface, giant kangaroo rats perform a valuable ecosystem service. Field biologist Joseph Grinnell (1877-1939), the first director of the Museum of Vertebrate Zoology at the University of California, Berkeley, once estimated that pocket gophers, excavating about 0.9 kilograms of soil per square meter (km^2), turned over 4,132 tons of soil every year in Yosemite National Park—a park comparable in size to the Carrizo Plain National Monument. In good years, giant kangaroo rats may cover 344 km^2 in the Carrizo, about half of which would be burrow mounds. Assuming a similar amount of worked-over ground—a conservative figure—that equates to over 17 *million* tons of soil. All of this excavating causes great changes to the soil chemistry, providing favorable habitat for a number of native plants. But their impact on the ecosystem goes beyond digging. Giant kangaroo rats are also great hoarders of seed. They can travel up to ten meters from their burrow mound to collect preferred seed, seed that they leave in hay piles to dry in the sun. The rats often bury the cured seeds in larder hordes within their burrows. But these hordes are susceptible to easy raids from neighbors. Therefore, kangaroo rats also bury handfuls of seed, superficially on the surface, in small pits. Moreover, giant kangaroo rats spend the majority of the early summer, after the green spring crop has dried, removing all vegetation from the top of their burrow mound. This behavior allows them to spot from further away such predators as the San Joaquin kit fox and to escape easily through open environments when they're attacked. These combined actions—soil perturbation and burrow building, vegetation removal, and seed caching—cause enormous changes to the ecosystem.

Seed removal isn't random. Giant kangaroo rats have dietary preferences, a mix of species: native (*Lepidium nitidum*, *Calandrinia ciliate,* and *Lasthenia californica*) and exotic (*Bromus madritensis* spp. *rubens*, and *Erodium cicutarium*). Consumption of these seeds directly reduces germination, roughly in order of preference—more preferred seeds germinate less often in areas where giant kangaroo rats are present. Perhaps surprisingly, soil perturbation has a more negative impact on germination than direct consumption of seeds. Soil properties also differ on giant kangaroo rat mounds, and these impacts linger even after the rats are gone. Calcium, electrical conductivity, bicarbonate, nitrogen, organic matter and pH are all higher on burrow mounds, while phosphorous and magnesium tend to be lower. These differences in the soil may lead to greater exotic plant establishment on giant kangaroo rat burrows, regardless of the species' presence.

But the impacts don't stop there. Not every spot of land where giant kangaroo rats are present is a burrow mound, and their foraging bouts don't take place everywhere. More vegetation is removed from the top of burrows than from surrounding areas. So while there are some fine-scale, negative impacts on native plant germination, these differences tend to reverse at larger scales. In fact, at a site level, giant kangaroo rat presence—through a combination of engineering effects, such as soil perturbation, and non-engineering effects, such as seed

predation—increases invertebrate biomass and diversity, plant productivity and diversity, as well as lizard and squirrel density. Again: at a burrow level, giant kangaroo rats negatively impact plant diversity, but at a site level, they increase overall plant productivity and diversity. When they are present at high abundance, they seem to compete with the California threatened San Joaquin antelope squirrel. But, the net effect of giant kangaroo rats on squirrels is positive as a result of the additional burrows they create and higher plant productivity.

Plant community dynamics are also complicated by desert/grassland conditions on the Carrizo Plain. In the spring, the Visitor's Center at the Carrizo Plain National Monument gets calls daily asking about the state of the wildflowers—as in the great California deserts, Carrizo benefits from an infrequent superbloom. But whether rainfall will trigger spectacular flower displays is highly speculative. Giant kangaroo rats make it even harder. The long-term exclosure experiment has demonstrated that the prior year's winter rainfall has a greater impact than the current year on plant productivity and composition. But giant kangaroo rat foraging mediates this impact and reduces the year-on-year changes in plant productivity and composition. In the absence of giant kangaroo rats, but where their burrows persist, exotic species, such as *Hordea murinum* and *Bromus madritensis* spp. *rubens*, benefit much more from higher rainfall in the previous year. Kangaroo rat foraging reduces this effect by increasing cover of native plants, which mediates the impact of high rainfall years that tend to favor exotic grasses.

The central challenge for organisms in arid environments isn't that it's dry all the time—it's the variability in rainfall. From 2007-2017, the annual centimeters of rain that the Carrizo received during the growing season are respectively: 10, 16, 17, 30, 40, 18, 9, 7, 13, 18, 28. Kangaroo rats can purportedly survive without freestanding water. Their strong kidneys and ability to create water by metabolizing seeds means they don't need much, if any, free water. Nitrogen concentration in their urine is closer to that of a bird or reptile than to most mammals. But the rest of a giant kangaroo rat's life history is dedicated to staving off drought. The burrow systems they build are, in essence, underground grain silos. The stored seed not only gets them through one winter, but potentially an entire year without new plant growth. In 2012, the year before the historic drought, giant kangaroo rat density in core habitat of the Carrizo was about fifty per hectare. In 2013, in the first year of the drought, it was down to about forty-three. In 2014, in the second straight year of severe drought and following a record dry winter, density crashed to less than five per hectare, and it remained low in 2015.

This decline in one endangered species set off a chain reaction for other rare rodents native to the San Joaquin desert/grassland. In core habitat, where more than 99 percent of all nocturnal rodents trapped are giant kangaroo rats, suddenly an entire community of small mammals emerged. Other kangaroo rats appeared: Heermann's, *D. heermanni*, and short-nosed, *D. nitratoides*. Two species of pocket mice, *Perognathus inornatus* and *P. californicus*, also invaded, as did the southern grasshopper mouse, *Onychoms torridus*, a species famous for its high-pitched "howls" and carnivorous diet. As the drought went on, this disruption extended up the food chain—wind scorpions, spiders, and the insectivorous blunt-nosed leopard lizard declined. Without the giant kangaroo rat to feed on, San Joaquin kit fox numbers dropped. Some plants suffered—native (yellow pincushion) and non-native (Arabian schismus), but others (San Joaquin woolly threads and red maids) flourished. Coast horned lizards and side-blotched lizards both did well in the drought, as did their main predator, the greater roadrunner, *Geococcyx californianus*. When the drought ended, giant kangaroo rats rebounded quickly. Rare summer rains in 2015 led to reproduction in August and September, and by 2017 densities were as high as ever. The other small mammals retreated. While the magnitude and length of the recent drought was anomalous, droughts are a fundamental feature of this ecosystem. The disruptive dry years seem to increase overall biodiversity by driving down common species and providing opportunities for rare ones.

Because the Carrizo Plain is halfway between a grassland and a desert, it hosts species that evolved in both worlds. Because it's halfway between two major mountain chains in the Coast Range, and halfway between the two largest cities in the state, it never received the irrigation that would have destroyed its native flora and fauna. Because it hasn't received the recognition of other protected areas to draw tourists, it hasn't been loved to death the way Yosemite has. Because it doesn't have quite the oil reserves as its cousins to the east, there's no heavy machinery. Halfway between everything else, the Carrizo Plain has carved out a niche as one of the most spectacular places for biodiversity conservation in the United States.

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