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SIXTEEN

History and Ecology of Feral Pig Invasions in California Grasslands

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Disturbance is a critically important factor influencing the structure of ecological systems and is considered integral to the maintenance of species diversity (Connell 1978; Grime 1979b; Huston 1979; Sousa 1984; Pickett and White 1985). However, both natural and human-caused disturbances are also widely recognized to facilitate the spread of exotic species (Mooney and Drake 1986; Drake et al. 1989; Hobbs and Huenneke 1992; D'Antonio and Vitousek 1992; D'Antonio et al. 1999; Sakai et al. 2001). In addition, exotic species themselves can greatly alter disturbance regime characteristics in their novel environments, either by enhancing or suppressing existing regimes or by introducing new forms of disturbance (Mack and D'Antonio 1998). Thus, disturbance in human-altered landscapes can pose significant challenges, particularly to vegetation management.

Biotic disturbance agents are important components of most ecosystems throughout the world and frequently modify local soil characteristics, plant community structure, and the dominance of exotic species (Hobbs and Huenneke 1992; Mack and D'Antonio 1998; Cushman et al. 2004; Tierney and Cushman 2006). Disturbances by native mammals—such as ground squirrels, kangaroo rats, moles, shrews, pocket gophers, prairie dogs, badgers, bears, and bison—create small-scale soil disturbances through burrowing, excavating, and wallowing that greatly alter the landscapes they inhabit (Platt 1975; Huntly and Inouye 1988; Whicker and Detling 1988; Hobbs et al. 1988; Lidicker 1989; Martinsen et al. 1990; Tardiff and Stanford 1998; Schiffman, Chapter 15). A growing number of studies document that such disturbances can facilitate invasion by exotic plant taxa, which rapidly colonize these openings (Rice 1987; Hobbs et al. 1988; Peart 1989c; Hobbs and Mooney 1991; D'Antonio 1993; McIntyre and Lavorel 1994).

Domesticated mammals have been introduced throughout the world, and many of these taxa have established feral populations, substantially altering prevailing disturbance regimes, and adversely impacted population, community, and ecosystem processes (Cox 1999; D'Antonio et al. 1999). Especially problematic have been feral goats *(Capra hircus)* and sheep *(Ovis aires)* on temperate and tropical islands (Coblentz 1978; Van Vuren and Coblentz 1987), feral horses *(Equus caballus)* and burros *(E. asinus)* in arid habitats of the western United States (Cox 1999; Beever and Brussard 2000; Beever et al. 2003), and feral pigs *(Sus scrofa)* on all continents except Antarctica, as well as many oceanic islands (Mayer and Brisbin 1991). The latter species greatly increases levels of disturbance by overturning extensive areas of vegetation and associated soil while foraging, thereby creating a mosaic of disturbance intensities and ages (Bratton 1975; Barrett 1978, 1993; Kotanen 1994, 1995; Cushman et al. 2004; Tierney and Cushman 2006).

Feral pigs are a prominent feature of grasslands in California and represent a challenge to management efforts in these landscapes. As touched on throughout this volume (especially in D'Antonio et al., Chapter 6), grasslands in California have undergone an extraordinary transformation in composition over the past two hundred years and are now dominated by a wide range of exotic plant species (Heady 1988; Heady et al. 1988; 1992). Thus, feral pigs are by no means the first invaders to colonize grasslands in California, but it is nevertheless critical to understand their impacts on these highly altered landscapes, particularly if restoration of native grassland composition is a desired goal.

In this chapter, I will explore the ecology and management of feral pig populations in the grasslands of California. Specifically, I will discuss (1) the history, taxonomy, geography, and basic ecology of feral pigs; (2) the response of native and exotic plant taxa from different functional groups to pig disturbances; (3) the impacts of pig disturbances on ecosystem processes; and (4) efforts to control or eradicate pig populations and manage grasslands in the face of invasion by these mammals. Although the focus will be on grasslands in California, studies from other regions or habitat types that are relevant to the discussion will also be considered.

Overview of Feral Pigs and Wild Boar

Native to Eurasia and North Africa, domestic pigs (*Sus scrofa domesticus*, Suidae) were brought to California by the Spaniards in the 1500s and were often allowed to forage freely in oak woodlands surrounding their settlements (Mayer and Brisbin 1991). As a result, by the late 1700s at least, many viable populations of pigs had become established in coastal areas, where settlements were most commonly located (Barrett 1978). In addition, Eurasian wild boar (*Sus scrofa scrofa*) were subsequently introduced for hunting into Monterey County in 1925 and other counties in the 1950s. These two subspecies readily interbreed, and populations in California are now a mixture of feral domestic pigs, wild boar, and various hybrids and backcrosses (Mayer and Brisbin 1991).

Wild pig populations in the state were restricted to a few coastal counties until the 1950s, but they expanded to 33 of California's 58 counties by the early 1980s. More recently, an analysis of hunting records by Waithman et al. (1999) found that the distribution of feral pigs increased from 10 coastal counties in the early 1960s to 49 of the 58 counties by 1996 (Figure 16.1). Until recently, pigs also occurred on four of the Channel Islands (Mayer and Brisbin 1991).

FIGURE 16.1. Estimated range and relative abundances of feral pigs in counties throughout California (Waithman et al. 1999). Black areas correspond to regions with high to very high densities; gray areas correspond to regions with moderate densities; and hatched areas correspond to regions with low densities (pigs are absent from white areas). Reprinted from the Journal of Wildlife Management.

The California Department of Fish and Game (CDFG) formally designated pigs a game mammal in 1957 (Tietje and Barrett 1993; Updike and Waithman 1996), and this status offered them partial protection from eradication and control efforts during an early stage in their invasion. In 1992, individuals were required to purchase license tags to hunt feral pigs in the wild, and revenue generated by CDFG from these sales—approximately 30,000 pigs are killed by hunters each year—are used to support research on the ecology and management of feral pigs (Updike and Waithman 1996).

Numerous factors undoubtedly contribute to the tremendous success of pigs outside of their native range (Barrett 1978; Mayer and Brisbin 1991; Waithman et al. 1999). First, humans have been rearing domesticated pigs for 8,000–9,000 years and have introduced them to many regions globally, where they frequently escaped or were intentionally released (Mayer and Brisbin 1991). Thus, there have been repeated introductions of this mammal throughout the world. Second, pigs are able to thrive in a wide range of habitats. For example, in California, they are common in oak woodlands, evergreen and mixed evergreen-hardwood forests and both grasslands and chaparral adjacent to forests. Third, pigs are efficient and very effective generalist foragers, moving rapidly among patches to capitalize on seasonal variation in resource availability. These opportunistic omnivores have an exceedingly diverse and variable diet that includes bulbs and roots, acorns, aboveground foliage of grasses and forbs, fungi, invertebrates, small vertebrates and carrion (Barrett 1978). Fourth, pigs have a high reproductive capacity, with each female producing 10–12 offspring per year, which enables populations to increase rapidly in size and promotes range expansion. Fifth, pigs commonly travel through the landscapes in groups (or sounders) of varying sizes. Groups are usually composed of females and their young, with males living on their own once they reach maturity and joining groups only for mating or to visit localized food or water sources. Such group behavior may increase their foraging success and/or reduce predation rates. Lastly, pigs learn quickly to avoid contact with humans and thus may be particularly elusive to hunters (Barrett et al. 1988).

Pigs exhibit distinctive foraging activity—often referred to as "rooting" or "grubbing"—that consists of excavating the soil to a depth of 5–15 cm (Kotanen 1994, 1995). The disturbed vegetation and associated soil may remain in place, or pigs may push this material to the side, thereby covering adjacent vegetation. As is widely reported in the literature, pigs can disturb large areas of vegetation and soil where they forage (Kotanen 1995; Sweitzer and Van Vuren 2002; Cushman et al. 2004), and Hone (2002) found that the area of land disturbed by pigs increased significantly with their density.

Responses of Grassland Vegetation to Pig Disturbances

Extensive published research has focused on the ecology, behavior, and management of pig populations in California (e.g., Barrett 1978; Waithman et al. 1999; Choquenot and Ruscoe 2003), but considerably less work has explored the impacts of pigs on plant, animal, or fungal populations or communities. Pigs can influence biota both directly and indirectly. Directly, feeding by pigs can adversely affect the survival and reproductive success of target species. The soil disturbances caused by pigs while foraging also directly kill or adversely affect a variety of species. Indirectly, these soil disturbances create openings in otherwise space-limited grasslands, which in turn affect resource availability, create opportunities for colonization, alter the dynamics of species interactions, and modify the composition and structure of communities. The relative importance of direct versus indirect effects of pigs would be difficult to determine. However, in most situations, the greatest effect of pigs probably comes from their soil disturbances, and much less from direct consumption of food species.

Studies in Australia, New Zealand, Hawaii, and the southeastern United States have suggested that foraging disturbances by pigs are associated with reduced dominance of native plants and increased abundance of exotic taxa (Bratton 1975; Challies 1975; Spatz and Mueller-Dombois 1975; Stone 1985; Aplet et al. 1991). In contrast, D'Antonio et al. (1999) have suggested that the effects of pig disturbances on grasslands in California may be less dramatic.

The most detailed research on the responses of plants in grasslands to feral pig disturbances has come from two sets of studies in northern California. In the first study, Kotanen (1994, 1995, 1996, 1997a, b, 2004) addressed the effects of actual and simulated pig disturbances on grasslands at the University of California's Angelo Coast Range Reserve in Mendocino County, 240 km north of San Francisco. A second set of studies (Cushman et al. 2004; Tierney and Cushman 2006) assessed the impacts of pig disturbances on grasslands at Salt Point State Park in northwest Sonoma County, 120 km north of San Francisco. These two detailed studies provide an opportunity to examine how consistent results are between sites because they are in close proximity to each other (only 120 km apart), and both involve coastal grasslands that occur in areas with high pig abundance (see Figure 16.1). However, there are numerous differences between these studies that complicate comparisons. First, although both sites are considered coastal grasslands, Salt Point is on the coast and subject to the ocean's moderating influence, whereas Angelo is farther inland and much hotter. Second, the two sites are different floristically, with Angelo dominated by native perennial bunchgrasses and exotic annual grasses, whereas Salt Point has an abundance of both exotic and native perennial grasses as well as exotic annual grasses. Third, Kotanen's research at Angelo was conducted primarily during 1990 to 1993 near the end of a six-year drought, whereas our work at Salt Point occurred from 1996 to 2000 when precipitation levels were more substantial. And fourth, the two sets of studies did not always quantify the same response variables.

Kotanen (1995) conducted a comparative study at the Angelo Reserve to assess how plant species richness associated with pig-disturbed areas differed from that in undisturbed areas. He found that pig disturbances initially reduced species richness during the first year after disturbance, and then richness rebounded to levels similar to or sometimes greater than those in undisturbed plots. Surprisingly, he also found that native and exotic richness responded similarly to pig disturbance. This result was due largely to the presence of many species of disturbance-dependent native annual dicots, which responded favorably to pig rooting. In another study, Kotanen (1997a) conducted an experiment to evaluate the responses of vegetation to simulated pig disturbances of different types and found that plant species richness either recovered three years following disturbance or was reduced, depending on the type of disturbance treatment applied. He also found that exotic annual grasses increased in abundance during the first three years following simulated disturbances but had decreased to low levels after 10 years (Kotanen 2004).

Cushman et al. (2004) conducted comparative and experimental studies at the Salt Point site to quantify the effects of pig disturbances on species richness and aboveground biomass of native and exotic plant taxa. The comparative study revealed that species richness and aboveground biomass of exotic plants increased significantly with increasing amounts of pig disturbance, whereas no such relationships emerged for native taxa. A four-year exclosure experiment showed that pig disturbances significantly decreased residual dry matter and increased plant species richness, especially for exotic taxa. Other studies have also found that small-scale soil disturbances by mammals can facilitate invasion by exotic plants, which possess life history characteristics that enable them to colonize and become established in these openings (Rice 1987; Hobbs et al. 1988; Peart 1989c; Hobbs and Mooney 1991; D'Antonio 1993; McIntyre and Lavorel 1994; Kotanen 1995, 1997a).

Results from Cushman et al.'s (2004) exclosure study for aboveground biomass were complex and varied greatly with plant functional group (annuals vs. perennials; grasses vs. forbs), geographic origin (native vs. exotic), and grassland type. The latter variable refers to two distinctive vegetation types that occurred extensively at the Salt Point site: a low-growing grassland vegetation dominated by annual grasses and forbs (the short-patch type) that was interspersed among areas of taller vegetation dominated by large perennial bunchgrasses (the tall-patch type). From a management perspective, two of the most encouraging results were that biomass of native perennial grasses (primarily *Deschampsia cespitosa* and *Danthonia californica*) was unaffected by pig disturbances in either patch type, and that biomass of exotic perennial grasses (primarily *Anthoxanthum odoratum*) was reduced significantly by disturbance in tall patches where they dominate (there was no effect in short patches). Cushman et al. observed that pigs rarely overturned established native bunchgrasses and hypothesized that this was due to the large size and deep roots of these individuals. At another nearby site, Peart (1989c) also found that pocket gophers tended to avoid areas dominated by bunchgrasses, and Kotanen (1995) found that native bunchgrasses were not adversely affected by pig disturbances. By contrast, individual exotic bunchgrasses at Salt Point were small in size, and Cushman et al. hypothesized that they lacked sufficient anchoring from root tissue to resist pig rooting.

The exclosure experiment conducted by Cushman et al. (2004) also revealed a number of outcomes that were negative from a management perspective. Pig disturbances increased aboveground biomass of exotic annual grasses *(Aira caryophyllea, Cynosurus echinatus, Vulpia myuros,* and *Briza minor)* in the short patch type where they dominate. These results were similar to the numerical increases found by Kotanen (1995) at the Angelo site. However undesired, such results are not surprising, given that exotic annual grasses are well known to respond positively to disturbance (see Hobbs and Huenneke 1992) and undoubtedly have a well-developed seed bank at the Salt Point site. The biomass of exotic forbs was also increased greatly by pig disturbance in tall patches. Like exotic annual grasses, these species possess life history characteristics that allow them to rapidly colonize the openings in grasslands that pigs create.

Tierney and Cushman (2006) used both comparative and manipulative approaches to assess how native and exotic vegetation at the Salt Point site changed through time following pig disturbances. The investigators quantified successional changes by comparing pig disturbances of varying ages (2, 14, 26+, and 60+ months old) and found that species richness of native plants increased slowly but steadily through time following disturbances, whereas richness of exotic species rebounded much more rapidly. Percent cover of native perennial grasses also increased steadily through time after pig disturbance, whereas the cover of exotic perennial grasses, annual grasses, and forbs initially increased rapidly after disturbance and then remained the same or subsided slightly with time. The cover of native forbs and bulbs either increased weakly through time following disturbance or did not change substantially. These results showed that native and exotic plants from different functional groups varied greatly in how they recovered from pig disturbance, with exotics generally able to colonize rapidly and persist in disturbances, whereas natives slowly but steadily rebounded following pig disturbance.

Two additional studies on the impacts of feral pigs in California warrant discussion. First, Peart (1994) conducted experiments on Santa Cruz Island in southern California and found that pig foraging and trampling reduced the abundance and survival of woody seedlings in grasslands and oak woodlands. She also found that the cover of native plants increased as a group when protected from pig disturbance, whereas the cover of exotics increased when exposed to disturbance. Second, Sweitzer and Van Vuren (2002) conducted comparative and experimental studies that assessed the effects of feral pigs on grasslands and oak woodlands at four sites in northern California: Austin Creek State Recreational Area in western Sonoma County; Sugarloaf Ridge State Park in eastern Sonoma County; McCormick Sanctuary in eastern Sonoma County; and Henry Coe State Park in Santa Clara County. Their comparative studies indicated that increasing amounts of pig rooting were associated with reduced aboveground plant biomass in grasslands. An exclosure study also showed that pig disturbances had no effect on the cover of native and exotic plant species at one grassland site (Austin Creek), whereas they increased the cover of exotics and had no effect on natives at another site (Henry Coe) (Sweitzer and Van Vuren, unpublished report). In addition, Sweitzer and Van Vuren found that pigs reduced the abundance of acorns on the ground, and increasing density of pigs was associated with reduced abundance of oak seedlings.

To conclude, the studies summarized in this section clearly indicate that feral pig populations can have pronounced impacts on the composition of grasslands in California. The emerging picture is that feral pigs promote the invasion of exotic plants in these habitats. However, the responses of plant communities to pig disturbance are context dependent and highly variable. The composition of disturbed plant communities plays a critical role in determining the overall response. In particular, the impact of pigs will be influenced greatly by the size and richness of native and exotic seed banks, the relative dominance of exotic annual grasses and native disturbance-responsive annuals, and the degree of coastal influence that a site experiences. Despite this complexity, the findings of Kotanen (2004) and Tierney and Cushman (2006) are encouraging because they suggest that native plant species can rebound considerably if protected from further soil disturbances. Thus, removing or reducing the size of pig populations—if feasible (see following discussions)—should be an effective technique for restoring native perennial grasses in coastal grasslands. Unfortunately, we suspect that this resiliency may be specific to coastal grasslands, where the long summer drought is tempered by maritime influences. The responses of more interior grasslands may differ greatly, with native plant groups being less able to recover from disturbances under the more arid conditions that prevail in these regions. The common exotic annual grasses in interior grasslands are different from those found in coastal systems and may be more aggressive competitors with native species. If such exotics are promoted by pig disturbance, they may lead to a greater suppressing effect on native species.

Impact of Pig Disturbances on Ecosystem Processes

Pig disturbances have the potential to indirectly influence a number of important ecosystem-level processes. They may increase soil mixing and alter rates of decomposition, mineralization, and nutrient retention. For example, Singer et al. (1984) found that intensive pig disturbances in a southeastern U.S. deciduous forest was associated with significantly greater nitrate, ammonium, and potassium pools in the soil. In a mesic forest on the island of Hawaii, Vitousek (1986) also found that net nitrogen mineralization was greater in pig-disturbed soils than in areas protected from disturbance for at least 14 years. In contrast to these results, Moody and Jones (2000) found no correlation between pig disturbances and changes in soil pH, moisture, nitrogen pools, or total carbon for oak savannas on Santa Cruz Island, off the coast of southern California.

What kinds of impacts have been detected for the two grassland sites in northern California discussed earlier? At Angelo Reserve, Kotanen (1997a) found that simulated pig disturbance did not significantly affect nitrate pools, and results for ammonium were somewhat equivocal: Levels were higher than controls for one type of simulated disturbance and lower for another. At Salt Point State Park, Cushman et al. (2004) found no evidence that pig disturbances affected nitrogen mineralization rates or soil moisture availability. At the same site, Tierney and Cushman (2006) also found that ammonium and nitrate pools and mineralization rates in the soil did not change greatly through time following pig disturbance, nor was organic matter content or particle size affected.

These results suggest that soil nutrients in northern California grasslands may not be greatly affected by pig disturbances. Numerous factors could explain the absence of effects. First, these grasslands may simply be able to withstand—or recover rapidly from—soil disturbances without experiencing significant changes in nitrogen availability. This might occur if nutrients do not leach rapidly from the system but instead collect in the many small depressions that pigs create. Another possibility is that grasslands have been intensively disturbed by pigs for many years and this has caused changes in soil characteristics prior to when the measurements occurred. Regardless of which factors are responsible, it seems that variation in soil characteristics cannot explain the many vegetation changes that investigators have detected. Instead, these results are more consistent with the hypothesis that changes in the plant community are caused by space clearing by pigs, which provides greater opportunities for colonization and reduced intensity of competition.

Population Control of Feral Pigs

Soil disturbances by feral pigs can have strong effects on grassland vegetation in California and lead to the further degradation of this already altered ecosystem. However, at least in coastal grasslands, the encouraging news is that native vegetation appears to rebound following pig disturbance, provided that additional disturbance does not occur. Thus, reducing or eliminating pigs and their impacts is key for the effective management of coastal grasslands, as well as more inland systems. However, once established, pig populations are difficult to eradicate, because of their high reproductive rate, their tolerance of diverse ecological conditions, and their ability to avoid contact with humans (Barrett et al. 1988; Waithman et al. 1999). In addition, although reductions in population size can be achieved, they are usually temporary; thus, control efforts must be viewed as continual activities.

Multiple techniques have been used to reduce the size of feral pig populations. Ground-based hunting by professionals has been an effective control method in some areas (Cruz et al. 2005), and sport hunters are the most widespread control method in California (R. H. Barrett, personal communication). Aerial-based hunting from helicopters can be effective in some areas, especially in open landscapes (Long 1993; Saunders 1993; Choquenot et al. 1999). Hunting with teams of dogs has also been effective after pig densities are reduced by other forms of control (Sterner and Barrett 1991; Caley and Ottley 1995). Snares can be an effective, albeit controversial, method and have been especially successful in extremely remote areas if other, larger native mammals are absent, as in Hawaii (Anderson and Stone 1993). Poisoned baits have also been used with success in Australia (Twigg et al. 2005), although they can be problematic if native species consume them as well. Whatever control method is used, success can be increased greatly when pig populations occur within fenced areas and their ability to leave the area is reduced or eliminated. Fencing is also critically important for preventing pigs from recolonizing areas that have been previously cleared of these animals (Barrett et al. 1988).

Complete eradication of feral pigs is usually considered possible only on islands or within fenced areas. For example, Cruz et al. (2005) reviewed the successful efforts to eradicate pigs from Santiago Island in the Galápagos Archipelago in Ecuador. During a 30-year period, over 18,000 pigs were removed from the island using a mixture of ground-based hunting and poisoning. The success of this eradication effort—which is the largest to date—was attributed to a sustained effort that used a combination of techniques and an intensive monitoring program. Another example comes from southern California, where intensive efforts have been mounted over multiple decades to eradicate feral pigs from four of the Channel Islands: San Clemente, Santa Catalina, Santa Cruz, and Santa Rosa. Pigs were eradicated successfully from San Clemente Island in the 1980s and from Santa Rosa Island in the 1990s (Long 1993). In contrast, the challenge has been more formidable for Santa Cruz and Santa Catalina Islands because of their larger size and more complex vegetation and terrain. In 1989, a study was initiated to assess the feasibility of eradicating pigs from Santa Cruz Island. Trapping, ground-based hunting, and hunting with dogs were all used to successfully eradicate pigs from a 2,250 hectare exclosure (Sterner and Barrett 1991). In 2005, The Nature Conservancy and the National Park Service initiated an effort to eradicate pigs from the entire island (L. A. Vermeer, personal communication). To facilitate this program, they divided the island into five zones using over 27 miles of pig fencing. A professional eradication firm from New Zealand was contracted to systematically remove pigs from each of the five zones. The eradication firm used a variety of techniques, phased over the course of the removal effort, including aerial hunting from a helicopter, use of large, humane corral traps, ground hunting in formation with tracking dogs, and radio-collared sentinel pigs (Morrison et al. 2007). On Santa Catalina Island, an intensive effort succeeded in eradicating pigs from a 38 square-kilometer fenced area between 1995 and 1997, but pigs still remain in others parts of the island (Garcelon et al. 1993).

Conclusions

Managing pig-invaded ecosystems is extremely complex because the soil disturbances that pigs create have a mixture of positive and negative effects on different components of a community. This situation highlights the increasingly common challenges that resource managers worldwide must face: They must simultaneously contend with multiple invaders that interact with each other and native taxa in complex and often unpredictable ways. Also, native taxa are heterogeneous in their responses to disturbances or management actions. Different functional or life form groups usually vary greatly in their responses to disturbance, and even members of the same functional group can behave differently as well. Such complexity and variability are not unique to feral pigs or grasslands in California and is discussed in other chapters; for example, variable responses of plant species to livestock grazing are described in Chapters 17 (Jackson and Bartolome) and 20 (Huntsinger et al.), and species-specific responses to climate-change manipulations are discussed in Chapter 19 (Dukes and Shaw). Such variability becomes most apparent when a community-level approach is taken that focuses on the responses of taxa from different functional groups and geographical origins. For understandable logistical reasons, ecologists and resource managers often shy away from such studies because they are labor-intensive and the data they generate are complex and often challenging to analyze statistically. Yet, to effectively and sustainably manage natural landscapes, it is necessary to embrace rigorous, science-based approaches that evaluate community-level effects of invasions and the responses to subsequent management actions.

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