Biology and Impacts of Pacific Islands Invasive Species. 14. *Sus scrofa*, the Feral Pig (Artiodactyla: Suidae)[1]

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Abstract: Feral pigs (*Sus scrofa* L.) are perhaps the most abundant, widespread, and economically significant large introduced vertebrate across the Pacific island region. Unlike many other nonnative invasive species, feral pigs have both cultural and recreational importance in the region, complicating their management. Today, Pacific island feral pigs are a mixture of several strains of domestic swine, Asiatic wild boar, and European wild boar. Due to their generalist diet and rooting behavior, feral pigs alter soils and watersheds and negatively impact native and nonnative flora and fauna. As a result, feral pigs have played a role in the extinction of several species of plants and animals on Pacific islands and have negative effects on both ecotourism and agricultural industries in the region. Despite numerous published studies on feral pigs in the Pacific island region, of which the majority include systematic analyses of original empirical data, some fundamental aspects of feral pig ecology remain poorly characterized, at least partly due to the remote and inaccessible environments that they often inhabit. To address these knowledge gaps, effort should be made to integrate research conducted outside the Pacific island region into local management strategies. This review summarizes the origins, history, ecology, environmental effects, and current management of feral pigs in the Pacific island region; integrates regional scientific findings with those of other insular and continental systems; and identifies current knowledge gaps requiring further research to inform the ecology and management of this impactful invasive species.

Keywords: ecology, environmental impacts, economic impacts, hunting, management, nonnative, ungulate

Anderson and Stone (1993:195) described feral pigs (*Sus scrofa* L.) as "the most pervasive and disruptive alien influence on the unique native forests of the Hawaiian islands." This quotation is representative of the wide-ranging effects feral pigs have globally, where they inhabit every continent except for Antarctica (Barrios-Garcia and Ballari 2012) and represent an invasive species in almost every part of their range. The widespread habitat degradation caused by feral pigs is unparalleled in the Pacific, and for more than 30 yr

[1] This material is based upon work supported by the College of Tropical Agriculture and Human Resources, University of Hawai'i at Mānoa via the USDA-NIFA Hatch (HAW01127H) and McIntyre Stennis (HAW01123M) Programs; and the Department of Defense Strategic Environmental Research and Development Program (RC-2433). Support for S.C.H. was provided by the Invasive Species program of the U.S. Geological Survey. Manuscript accepted 12 September 2017.

Pacific Science (2018), vol. 72, no. 2:177–198
doi:10.2984/72.2.1

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management of feral pigs has been limited only by the availability of funding and policies reflecting public sentiment, including advocacy by both hunters and cultural practitioners. Management projects have focused primarily on fencing and removal in conservation areas throughout the region to minimize habitat degradation associated with feral pigs (Tomich 1986).

Feral pigs are unique because undomesticated populations of *S. scrofa* still existed in the wild when domesticated pigs first became feral (Diong 1982). In addition, *S. scrofa* interbreeds with other members of the *Sus* genus, furthering the distinctive nature of this species. Overall, *S. scrofa*'s existence as wild, feral, domestic, and interbred forms has caused a great deal of confusion regarding their taxonomy (Diong 1982, Moutou and Pastoret 2010). Recently, the implementation of genetic tests to differentiate between wild, feral, and domestic lineages has allowed researchers to track historical introductions of individual populations (Aravena et al. 2015, Linderholm et al. 2016), and further implementation of this strategy in the Pacific represents an opportunity to fill important knowledge gaps clarifying feral pig introductions and their taxonomic status.

NAME

Sus scrofa (Linnaeus, 1758)

Common names: feral hog, pig, or swine; Old-World swine; razorback; Eurasian or Russian wild boar or hog.

It is important to clarify that the term "feral pig" is representative of those populations descended from historically domesticated populations. In Europe and Asia, undomesticated lineages of wild boar still exist. However, suides throughout the Pacific should generally be recognized as feral because nearly all pig populations in the Pacific are genetic hybrids of domestic, feral, and, on some islands, wild populations that may never

Figure 1. Lactating feral pig, *Sus scrofa*, on Hawai'i Island. (Photo: U.S. Geological Survey.)

have been domesticated (Diong 1982). This distinction often causes confusion due to the interchanging use of common names for feral pigs.

LIFE HISTORY TRAITS

Feral pigs are considered Old-World swine, but they have been widely distributed in the New World due to domestication (Diong 1982, Graves 1984). As newborns, piglets stand minutes after birth and begin forming dominance relationships with their siblings within hours (Graves 1984). Worldwide, juvenile feral pigs are generally all black, but additional varieties include a wild type with reddish striping. As adults, feral pigs have a sparse but highly coarse coat, which is usually all black (Graves 1984, Long 2003). However, occasional spotting and/or white feet occur in adults. These coloration patterns are indicative of remnant genetic traits from prior domestication (Tomich 1986). Adult feral pigs have upward curving canine teeth, which form tusks in males (Giffin 1978, Graves 1984). On average, feral pigs weigh between 45 and 70 kg in the Pacific island region, but cases have been reported of females reaching weights of 90 kg and males reaching up to 250 kg (Giffin 1978).

Historically, domestic pigs were bred to maximize growth rate and reach maturity quickly (Lega et al. 2016), and female pigs can begin reproducing in their first year (Taylor et al. 1998). Once they become reproductively active, a Texas study showed that feral pigs generally became pregnant every 21 months, with roughly 40% of all females becoming pregnant each year (Taylor et al. 1998). However, it is possible for two litters to be born per year under ideal conditions, as is frequently the case in the Pacific, where feral pigs breed year-round (Diong 1982). A study of feral pigs in Hawai‘i showed that 24% of 327 females sampled were pregnant, with a median number of seven embryos per pregnant sow (Hess et al. 2006), and a Costa Rican study showed that 46% of all females sampled were either pregnant or suckling (Sierra 2001). Socially, the reproductive habits of feral pigs include moderate levels of polygyny but almost no polyandry (Hampton et al., A preliminary, 2004). Among feral pigs, older, heavier females became pregnant more often than their younger, smaller counterparts, with those older, larger females producing larger litters (Taylor et al. 1998, Fonseca et al. 2011). Typically, litter sizes consist of five or six piglets and show a slight bias toward being male (Diong 1982, Taylor et al. 1998, Fonseca et al. 2011).

Feral pigs live in matrilineal groups known as “sounders.” Sounders are composed of several generations of related females and their dependent offspring (Gabor et al. 1999, Kaminski et al. 2005). These sounders, however, are generally confined to a single family unit and therefore not considered to be herds (Graves 1984). At their maximum size, large sounders may reach 30–50 individuals, with some rare cases of sounders as large as 400 pigs having been observed (Long 2003). However, sounders are frequently smaller, and within larger sounders it is common for subgroups to form (Gabor et al. 1999). Generally, sounders are stable social units, with most female offspring remaining with the sounder after weaning (Boitani et al. 1994, Kaminski et al. 2005). Sounders can have territorially exclusive, nonoverlapping core home ranges (Sparklin et al. 2009). However, feral pigs do not defend their home ranges from other sounders, and individuals within sounders often have nonexclusive, overlapping home ranges (Graves 1984, Sparklin et al. 2009). It is therefore likely that movement between sounders facilitates gene flow (Hampton et al., Molecular, 2004).

Little information is available regarding the size of feral pig home ranges and distance of juvenile dispersal, especially on Pacific islands. A single study conducted in Hawai‘i estimated feral pig home ranges using four individuals. The resultant Global Positioning System (GPS) telemetry data produced home ranges between 0.11 and 0.86 km^2 (Salbosa 2009). In New Zealand, home ranges were shown to be somewhat larger, covering 0.3 to 2.1 km^2 (McIlroy 1989). In contrast, a study conducted in Texas calculated average home range for females much larger than those on Pacific islands, ranging between 4.6 to 6.1 km^2 with core ranges of 2.7 to 3.1 km^2, with the smaller ranges on Pacific islands likely due to the high concentration of food resources available there (Hampton et al., Molecular, 2004). In terms of juvenile dispersal, a Polish study suggested that, although some movement between sounders occurs, dispersal ranges are generally similar to home ranges, indicating that juveniles remain within their birth sounders (Podgorski et al. 2014).

Population sizes are difficult to estimate, but several techniques have been used including damage transects (Hess et al. 2006, Leopold et al. 2016), predictive modeling (Holland et al. 2009), and feces counts (Ferretti et al. 2016). Random encounter models that do not require specific individual recognition have the potential to more accurately estimate feral pig populations in the Pacific (Rowcliffe et al. 2008). However, those models are not currently used on Pacific islands due to the rugged and heavily vegetated terrain present on many islands. Other techniques being employed include DNA analyses, aerial surveys, mark/recapture, and hunter surveys (Engeman et al. 2013). Despite difficulties in estimating population densities, an Australian study estimated average densities of 12 to 43 pigs per km^2 in areas without hunting compared to densities of 3 to 8 pigs per km^2 in nearby heavily hunted sites (McIlroy 1989). In Hawai‘i, Scheffler et al. (2012) estimated population densities between 0.6 and 16.3 feral pigs per km^2. Variation in reported population densities of feral pigs is likely dependent on food availability, with reproductive habits often mirroring mast seeding/fruiting events (Graves 1984, Salinas et al. 2015).

Feral pigs are well-known for two primary behaviors: wallowing and rooting (Figure 2). Feral pigs can create large wallows many meters wide, where the primary use of wallows is to help remove parasites from the hide, heal cuts, and create a protective lathering of mud against pests (Graves 1984, Campbell and Long 2009). Some research has also suggested that wallowing may serve a role in obtaining mates because older, stronger males are seen wallowing more frequently during reproductive periods (Fernandez-Llario 2005). Wallows are destructive, creating bare patches throughout the landscape. Similarly, feral pig rooting behaviors lead to habitat degradation. Rooting is one of the primary foraging strategies utilized by feral pigs and involves digging or scraping into the top layer of soil to obtain food, particularly earthworms and plant roots (Lincoln 2014). On average, the pits resulting from feral pig rooting are approximately 10 cm deep (Hancock et al. 2015), and in tropical wet forests an individual rooting pig can disturb up to 200 m^2 of soil each day (Anderson and Stone 1993).

In terms of their diet, feral pigs are opportunistic omnivores relying primarily on their sense of smell to locate forage, and numerous studies have highlighted their wide-ranging diets. For example, a 7 yr study in Texas showed that around 40% of all feral pigs sampled had vertebrates, mostly carrion, in their stomach contents, which the authors attributed to the scarcity of easily obtained protein in the summer and fall (Wilcox and Van Vuren 2009). By comparison, a New Zealand population was shown to obtain up to 27% of its diet from underground invertebrate species alone (Parkes et al. 2015). In Costa Rica, feral pig diets were primarily composed of fruit regardless of the season (Sierra 2001), and Argentinian feral pigs had diets comprising 95% vegetation (Cuevas et al. 2010). A study in Pakistan showed that *S. scrofa* obtained 58% of their diet from garbage (Hafeez et al. 2011), a testament to their omnivorous habits. In Hawai‘i, Diong (1982) showed that the three most common food sources by volume for feral pigs were tree ferns (*Cibotium* spp.), strawberry guava fruit (*Psidium cattleianum*), and earthworms. Due to the opportunistic feeding habits of feral pigs, agricultural crops can also represent a large portion of their diet. Examples given include feral pigs that obtained 25% of their diet from sugarcane (Wurster et al. 2012), and a separate study showing that one-third of all feral pigs near sugar beet fields relied on beets for >50% of their diet (Zeman et al. 2016).

HISTORY OF INTRODUCTIONS

Globally, feral pigs inhabit every continent excluding Antarctica (Long 2003, Barrios-

Figure 2. *Top*, a feral pig wallow on the island of Hawai'i; *bottom*, feral pig rooting (*right*) versus forest understory with feral pig exclusion (*left*).

Garcia and Ballari 2012). Even within the native range of undomesticated wild boar, numerous releases of feral pigs have led to interbreeding between the two groups. The domestication of *S. scrofa* originally occurred in Europe to utilize wild boar for agricultural husbandry (Moutou and Pastoret 2010). As such, Europe became one of the first places to experience the effects of feral pigs after domesticated *S. scrofa* returned to the wild (Wilson 2004). With European trade expansion, domesticated pigs began to spread across the world and became a prominent food source for expanding human populations. It is important to note that, before the advent of contemporary methods using genetic techniques and mitochondrial DNA, the phylogeography of Suidae was based solely on comparative morphology of skeletal remains compared with modern specimens, cytogenetic determination, and utilization of other less-informative characteristics such as the presence of facial warts. Conclusive phylogenetic work has only recently become available with the use of genetic tests to differentiate between wild, feral, and domestic lineages and track historical introductions of individual populations (Aravena et al. 2015, Linderholm et al. 2016).

The history of feral pigs on Pacific islands originates in Island Southeast Asia with the oceanic voyages of the Neolithic Lapita culture, ancestors of the Polynesians (Larson et al. 2005). All five *Sus* species endemic to Island Southeast Asia (*S. barbutus*, *S. celebensis*, *S. philippensis*, *S. scrofa*, and *S. verrucosus*) originated from the region including the Malay Peninsula, Sumatra, Java, Borneo, and the Philippines. Two separate human-mediated dispersals of domestic pigs from Island Southeast Asia into Oceania have been documented using mitochondrial DNA from ancient and modern pig specimens (Larson et al. 2007). A Pacific clade of *S. scrofa* was dispersed from mainland Southeast Asia to Java, Sumatra, and the islands of Wallacea and Oceania, with a separate dispersal occurring with the translocation of *S. scrofa* from mainland East Asia to western Micronesia, Taiwan, and the Philippines. The first appearance of *S. scrofa* in Wallacea is closely associated with the arrival of the Lapita culture between 5000 and 1500 BC.

Evidence suggests that domesticated *S. scrofa* were not brought to the Hawaiian Islands by Polynesian voyagers until between AD 1000 and 1200 (Dye and Pantaleo 2010, Kirch 2011). This evidence arose from recent radiocarbon dating from an archeological site at Bellows, Oʻahu (Dye and Pantaleo 2010), corroborated by data suggesting that Pololū Valley on Hawaiʻi Island was first settled by Polynesians between AD 1200 and 1300 (Field and Graves 2008). In addition, Burney et al. (2001) documented pig bones from prehistoric habitation near a sinkhole and cave system on Kauaʻi dating from AD 1430 to 1665, well before the arrival of Europeans. Pigs did not, however, reach Australia and New Zealand until the age of European exploration through Polynesia in the late 1700s, which brought European *S. scrofa* to numerous islands throughout the Pacific (Clarke and Dzieciolowski 1991, Gongora et al. 2004).

Both skeletal remains of pigs and early historic observers indicate puaʻa (the Polynesian lineage of *S. scrofa*) were smaller than contemporary feral pigs in Hawaiʻi, weighing only 27 to 45 kg (Ziegler 2002). It was historically related that, not long before European contact, well over a thousand animals would be consumed at the consecration of important heiau (temples). Following European contact, Captain James Cook's voyage was provisioned with ~600 pigs during a 4-month stay in Hawaiʻi in 1778–1779. Later, Captain Cook noted that, when trading for pigs, "We could seldom get any above fifty or sixty pounds weight" (Diong 1982:53). In 1823, Missionary William Ellis observed that natives possessed "a small species of hogs, with long heads and small erect ears" (Ellis 1827:33), which further confirms a Polynesian origin of pigs in Hawaiʻi. This information regarding the historic ranges of feral pigs provides reason to believe that puaʻa brought by the original Hawaiian settlers differed substantially from the feral pigs found in Hawaiʻi today.

Originally, puaʻa had close relationships with humans and are believed to have stayed close to the kauhale (family compound) where taro and sweet potato agriculture was well developed (Maly et al. 1998). Before European contact, Polynesian man-pig interactions were essentially loose, with Ellis (1827:71) stating that pigs were "never confined in sites, but range about in search of food." Similarly, Cook observed pigs as abundant, forming an important part of the natives' culture, and further noting, "The pigs, herded with dogs, acted as scavengers and were left unattended to roam freely and without restraint" (Diong 1982:70). This traditional and historic evidence indicates that pua'a remained largely domesticated, living on the periphery of kauhale and extending no farther than nearby lowland forests (Ziegler 2002). They relied largely on the food and shelter provided by the kauhale because, in pre-contact times, native Hawaiian forests were devoid of large nonnative fruits such as mangos (*Mangifera indica*) and strawberry guava (*Psidium cattleianum*), as well as major sources of protein that would eventually support the large populations of feral pigs today (e.g., nonnative earthworms). Without such fodder, early roaming populations would have been chiefly dependent on people for food and survival. Therefore, it is highly likely that small populations of loosely controlled and free-roaming animals existed historically (Ziegler 2002).

Domesticated pua'a carried strong cultural value in traditional Polynesian cultures. Aside from being an important possession and food source, oral tradition describes the adventures of Kamapua'a (the pig god) in Hawai'i, a powerful demigod who ranged over the Islands and into the sea (Charlot 1987). Even the name of the traditional land management system in Hawai'i (ahupua'a) refers directly to the pua'a, highlighting their importance amongst the resources collected and given as offerings during annual makahiki (festivals). However, pua'a were not hunted as game by ancient Polynesians. Instead, the Polynesians' interaction with pua'a was one of near-complete domestication (Ziegler 2002). Despite references to hunting rats with bow and arrows, no historic or traditional knowledge sources describe ancient Hawaiians hunting pigs for food or recreation. Even in the legend of Kamapua'a, where the demigod is pursued by man, he is sought so that he might be punished for his mischievous actions, not for sport or sustenance (Charlot 1987).

Today, a cultural shift has taken place where recreational hunters strongly support the presence of feral pigs in the Hawaiian Islands for sport and sustenance, and conservation biologists consider their removal as a prerequisite step for protecting native vegetation. There are segments of current-day society who argue that pigs and other ungulates serve a historically and culturally important role and, as such, should be allowed to roam freely (Ikagawa 2013), often citing unverifiable information to support this viewpoint. Our goal is not to debase the cultural and recreational importance of feral pigs in the Pacific island region, but rather to summarize existing information regarding their impacts. First, conservation and restoration projects on Pacific islands promoting native vegetation are severely hampered by the presence of ungulates (Reeser and Harry 2005, Cole and Litton 2014, Hess 2016). Second, the pigs inhabiting the islands alongside original Polynesian settlers were smaller and more easily controlled, serving as localized food sources that were not explicitly hunted (Ellis 1827). Finally, the influx of invasive plants, as well as interbreeding with larger European pigs following the arrival of Captain Cook, has led to an expansion of negative impacts generated by feral pigs on Pacific islands.

Inevitably, debate over these viewpoints arises at least in part regarding the genetic purity of feral pigs as entirely European *S. scrofa*. Evidence suggests that Pacific island feral pigs are derived from multiple lineages, and the number of chromosomes in crossbred pigs ranges from 36 to 38, depending on the combination of Asiatic, European, domestic, and hybridized backgrounds of individuals (Giffin 1978, Diong 1982). It is therefore important to clarify that feral pigs on Pacific islands should be recognized as feral *S. scrofa*. Recently, Linderholm et al. (2016) showed that ~70% of the genetic makeup of feral pigs tested in Hawai'i came from *S. scrofa* of Polynesian ancestry. The hunting community used this information to argue that feral pigs should not be removed from Hawaiian islands. However, that study drew inference from the investigation of only one allele among a relatively small sample of *S. scrofa* (57 pigs sampled across four islands). We therefore conclude that more comprehensive genetic work needs to be conducted to be able to draw conclusions regarding feral pig genetics in the Pacific region.

GEOGRAPHIC DISTRIBUTIONS

In the Pacific, feral pigs inhabit nearly every island throughout the region (Table 1). Only the Cocos Islands (Woodroffe and Berry 1994), Easter Island (Allen et al. 2001, Giovas 2006), Pitcairn Island (Giovas 2006), and Wake Island (Griffiths et al. 2014) were recorded as being devoid of feral pigs. However, it is important to note that these four islands likely had pigs introduced at some point, but due to a general lack of resources and distance from other land masses, feral pigs likely never established there (Allen et al. 2001). Further, we assume that feral pigs are not present on Cocos and Wake Islands because they were not listed among other mammals described in literature from those respective locations (Woodroffe and Berry 1994, Griffiths et al. 2014).

Globally, feral pigs are one of the most widespread invasive species on the planet. This diaspora is primarily due to their generalist diet and ability to live in variable climates (Campbell and Long 2009), as well as their historic utility to humans. Generally, feral pigs show an inability to withstand harsh winters experienced in polar climates or hot summers of desert regions. However, a poleward shift in continental populations is occurring, likely due to current climate change, and microclimate exceptions do exist (McClure et al. 2015).

TABLE 1

Presence of Feral Pigs on Select Pacific Islands

Pacific Islands	Present	Absent	Notes
American Samoa	X[a]		
Australia	X[a,b]		
Bonin Islands	X[c]		
Cocos Islands		X[d]	
Easter Island		X[e]	
Fiji	X[a,b]		
French Polynesia	X[a,b]		
Galápagos Islands	X[a,b]		
Guam	X[a,b]		
Hawaiian Islands	X[a,b]		
Indonesia	X[a,b]		
Japan	X[a,b]		
Juan Fernández	X[a,b]		
Kiribati	X[a]		
Marshall Islands	X[a]		
Micronesia	X[a]		
Nauru	X[a]		
New Caledonia	X[a,b]		
New Zealand	X[a,b]		
Niue	X[a]		
Norfolk Island	X[b]		
Northern Mariana Islands	X[a,b]		
Palau	X[a,b]		
Papua New Guinea	X[a,b]		
Philippines	X[f]		
Pitcairn Island		X[e]	
Solomon Islands	X[a,b]		
Taiwan	X[a]		
Tokelau Islands	X[b]		Loosely domestic[b]
Tonga	X[a,b]		
Tuvalu	X[g]		Loosely domestic[g]
Vanuatu	X[b]		
Wake Island		X[h]	
Wallis and Futuna	X[a]		

[a] Barrios-Garcia and Ballari (2012).
[b] Long (2003).
[c] Kawakami and Okochi (2010).
[d] Woodroffe and Berry (1994), New World Encyclopedia Contributors (2017).
[e] Allen et al. (2001), Giovas (2006).
[f] Oliver (2014).
[g] McKinnon (2009).
[h] Griffiths et al. (2014).

DEGRADATION OF NATURAL ENVIRONMENTS

Feral pigs are well-known for their role as ecosystem engineers, and they generate impacts at multiple trophic levels across both localized and landscape spatial scales (Barrios-Garcia and Ballari 2012, Hess 2016). Although few studies have accurately determined pig abundance beyond presence or absence, their impacts have been demonstrated throughout the Pacific, largely via comparisons of habitats inside and outside fenced feral pig removal units (Cole et al. 2012, Cole and Litton 2014).

Impacts on Fauna

It is possible to extrapolate impacts from the degradation of natural environments and ecosystem-level impacts, but there are few studies in the Pacific examining the direct effects of feral pigs on other fauna. However, one noteworthy direct effect is egg predation and the destruction of important nesting sites used by Pacific island ground-nesting avifauna (Challies 1975). In addition, one indirect effect widely reported in Hawai‘i is the spread of avian malaria with feral pig activity. Specifically, wallowing and rooting behaviors create pools of standing water that provide habitat for nonnative mosquitoes carrying avian malaria, and a lack of resistance to avian malaria in native Hawaiian forest birds has resulted in remarkable population reductions and even extinctions of numerous endemic avifauna (Atkinson and LaPointe 2009). Climate change, particularly rising temperatures that allow mosquitoes to expand habitat into higher-elevation, mosquito-free zones, poses an immediate extinction threat for remaining forest bird populations in Hawai‘i, especially on lower-elevation islands (Paxton et al. 2016).

Beyond avifauna, feral pigs affect many other animals. For example, compaction of soils has been shown to negatively impact arthropod communities (Vtorov 1993), but feral pigs have also been shown to aid in dispersing aquatic invertebrates (Vanschoenwinkel et al. 2008). Additional negative effects include the destruction of turtle habitats in Australia stemming from trampling in mudflats surrounding marshes (Doupé et al. 2009); outcompeting of native peccaries in Texas (Galetti et al. 2015) and Brazil (Keuroghlian et al. 2009); and outcompeting of fox populations in California (Melstrom 2014). Other direct impacts on fauna and indirect effects on freshwater and marine communities due to soil erosion and sedimentation are likely, but largely unknown.

Impacts on Flora

The remote location of many Pacific islands prevented most terrestrial mammals from colonizing those habitats historically. Now, due to anthropogenic transport, these island ecosystems face an inundation of nonnative mammals such as feral pigs (Hess 2016), which are typically highly destructive to native vegetation (Aplet et al. 1991). Before the introduction of mammals to Hawai‘i, for example, terrestrial herbivores comprised snails, insects, and flightless birds, with only two species of bats representing native terrestrial mammals (Ziegler 2002). Defense against herbivory arose in at least 10 native Hawaiian plant species (Olson and James 1982, Givnish et al. 1994). However, due to the absence of terrestrial mammalian herbivores, especially ungulates, many Hawaiian plant species lost evolved defenses to mammalian herbivory, such as woody thorns, stinging nettles, and alkaloids (Carlquist 1970, Bowen and Van Vuren 1997). As such, direct herbivory can cause dramatic damage to Pacific island plant communities. Feral pigs are known to consume the roots, buds, flowers, and fruits of plants (Diong 1982, Ralph and Maxwell 1984, Tomich 1986, Katahira et al. 1993, Pratt et al. 1999, Cole and Litton 2014), and up to 95% of feral pigs' diets seasonally can come directly from vegetation (Diong 1982, Cuevas et al. 2010). Feral pigs are also well-established seed predators, limiting the recruitment of some plant species, particularly in continental mast-seeding environments (Lott et al. 1995, Sweitzer and Van Vuren 2008, Sanguinetti and Kitzberger 2010). In turn, feral pigs readily disburse many nonnative seeds, particularly those found in fleshy fruits (Diong 1982).

Feral pigs damage plants via rooting, in addition to direct herbivory. Rooting behaviors cause extensive damage to both seedlings and adult plants (Diong 1982, Campbell and Long 2009, Cole et al. 2012, Cole and Litton 2014, Murphy et al. 2014). The impact of feral pigs on seedlings is exemplified by an experiment analyzing the role of small-scale physical disturbance in seedling mortality in a Hawaiian rain forest. After 1 yr, the percentage of seedlings damaged was significantly greater among terrestrial seedlings versus epiphytic seedlings in the presence of feral pigs, and significantly more terrestrial seedlings were damaged with feral pigs present (Drake and Pratt 2001).

Direct damage to plants can also result from nest building (Ickes et al. 2005), trampling, wallowing, and rubbing on trees and other woody plants to remove skin parasites (Murphy et al. 2014).

One of the most notable effects of feral pig damage to native plant communities is the potential for native plants to be replaced by nonnative, invasive plants. An examination of the association between feral pig disturbance and the composition of nonnative plant assemblages in Hawai‘i Volcanoes National Park suggested a strong relationship between feral pig activity and nonnative plant presence (Aplet et al. 1991). For example, many mesic and wet forests in Hawai‘i are being inundated by the highly invasive strawberry guava, which is thought to have expanded dramatically due to feral pig activity (Diong 1982, Aplet et al. 1991). Feral pigs eat strawberry guava fruits and then release the seeds via their feces, providing excellent conditions for further recruitment and dispersal (Diong 1982, Huenneke and Vitousek 1990). Other invasive plants known to be spread by feral pigs in the Pacific region include banana poka (*Passiflora tarminiana*) (Beavon and Kelly 2015), mesquite (*Prosopis pallida*) (Lynes and Campbell 2000), and the freshwater pond apple (*Annona glabra*) (Setter et al. 2002), all of which show high levels of germination or recruitment following feral pig–mediated dispersal. The replacement of native plants with invasive plants due to feral pig activity results in a positive feedback loop generating progressively more opportunities for invasive plants to establish, which may, in turn, alter wildfire regimes (Trauernicht et al. 2015).

Following the removal of feral pigs via exclusion fencing, plant species recover quickly where they still exist at the time of removal (Spear and Chown 2009). Using a chronosequence of feral pig removal, Cole and Litton (2014) found that common understory native vegetation recovered within 6.5 yr of feral pig removal from Hawaiian tropical montane wet forests. Similarly, Weller et al. (2011) showed improvement among at least some native plants following ungulate removal from Hawaiian mesic forests, and Busby et al. (2010) showed improved native seedling survival inside ungulate exclosures in Hawaiian wet forests. Another study in wet-forest habitat in Hawai‘i Volcanoes National Park documented that feral pig removal increased native understory cover by 48% in 7 yr, with most recovery occurring in the first 2 yr following feral pig removal (Loh and Tunison 1999). A reexamination of these plots 16 yr after feral pig removal documented extended recovery of commonly occurring native understory woody plants (Cole et al. 2012). Importantly, these studies documented that nonnative plants also benefited from feral pig removal, with as much as a 190% increase in nonnative understory vegetation cover following removal (Loh and Tunison 1999, Cole et al. 2012). The important takeaway from these studies is that once feral pigs are removed, all plants that are present seem to benefit as a result of release from top-down control, regardless of whether the plants are native.

Impacts on Soils

Broadly speaking, the effects of feral pigs on the physical, chemical, and biological properties of soils are much less well understood than their aboveground impacts (Spear and Chown 2009, Long et al. 2017). Feral pigs primarily impact soils through trampling, wallowing, and rooting, as well as the deposition of feces and urine and aboveground impacts on plant communities. The presence of feral pigs can alter soil structure via reduced aggregate stability and increased compaction (Beever et al. 2006, Long et al. 2017), which can in turn affect arthropod communities (Vtorov 1993). Further, the degradation of understory plant communities can lead to long-term impacts on soils given the close linkages between above- and belowground biota (Wardle et al. 2004). Wallowing, much like trampling, leads to increased soil bulk density (Bueno et al. 2013) and can also affect soil structure by creating depressions that allow water to pool.

Feral pigs have been shown to alter soils differently in various habitats. For example, in Tennessee’s deciduous forests, soil bulk density was decreased by feral pigs (Singer et al. 1984), but soil bulk density increased with feral pig presence in Spanish alpine habitats (Bueno et al. 2013). Removal of feral pigs from Hawaiian wet forests resulted in decreased soil bulk density within 6.5 yr (Long et al. 2017). Physical alteration of soil organic matter via fragmentation during feral pig foraging was also recorded in some (Hobbs 1996, Siemann et al. 2009, Wirthner et al. 2012), but not all cases (Bruinderink and Hazebroek 1996). Feral pigs variably impact soil nutrient cycling and availability as well, with several studies documenting increased soil nitrogen with feral pig activity (Siemann et al. 2009, Wirthner et al. 2012, Bueno et al. 2013), but others have observed increased cycling and availability of soil nitrogen with feral pig removal (Long et al. 2017). Variability in the impacts of feral pigs on soil properties may result from methodological differences across disparate studies (Davidson and Hewitt 2014, Long et al. 2017).

Rooting is a common foraging activity used by feral pigs to support specific dietary needs. As a result, during foraging activities individual feral pigs can generate pits roughly 10 cm deep over up to 200 m^2 of soil daily (Anderson and Stone 1993, Hancock et al. 2015). Feral pigs prefer sandy soils for rooting over those composed of clay or rock because of the ease of access (Elledge et al. 2013). Further, it has been documented that feral pigs exhibit a strong propensity to root in places where the soil has been previously disturbed (Elledge et al. 2013, Hancock et al. 2015, Krull et al. 2016). The return of feral pigs to previously disturbed sites is important because it indicates a positive feedback loop leading to continued soil degradation. A potential facilitative relationship between feral pigs and earthworms may explain why feral pigs preferentially return to sites with disturbed soils. Supporting this concept, studies in Hawai‘i and Australia correlated worm abundance and feral pig activity (Taylor et al. 2011, Lincoln 2014), and in Spain rooting disturbance was shown to directly increase the abundance and diversity of earthworm species (Bueno and Jimenez 2014). However, a Slovenian study suggested the increased presence of earthworms did not lead to increased damage by feral pigs due to their highly opportunistic foraging strategy (Laznik and Trdan 2014). It is important to further understand the ecological implications of potential interactions between feral pigs and earthworms, particularly in the Pacific region, where earthworms are largely nonnative.

Associated with soil disturbance, feral pigs are known to generate numerous negative effects on watersheds. These effects include increased soil erosion and runoff, thereby decreasing water quality at multiple scales (Browning et al. 2008, Cuevas et al. 2010, Doupé et al. 2010, Strauch et al. 2016). For example, feral pig–associated runoff results in elevated nitrogen levels (Cuevas et al. 2010, Strauch et al. 2016) and increased acidity in nearby water, which can occur over extended periods of time (Doupé et al. 2009). In addition, increased downstream sedimentation rates have been traced to feral pig activity (Dunkell et al., Runoff, 2011), as has alteration of wetland plant communities (Arrington et al. 1999, Setter et al. 2002). Feral pig activity has also been associated with the presence of fecal matter in watersheds (Strauch et al. 2016), increased levels of enterococci (Browning et al. 2008; Dunkell et al., Effects, 2011; Bovino-Agostini et al. 2012), and the presence of leptospira (Browning et al. 2008).

ECONOMIC IMPORTANCE

Due to the longstanding importance of feral pigs as a cultural icon in the Pacific, putting a direct price on their value is difficult. Culturally, feral pigs serve an important role in the folklore and traditions of contemporary native peoples (Charlot 1987). Further, the species today is important to hunters throughout the Pacific, who view it as a primary target for recreation and sustenance. Based on current harvest numbers for Hawai‘i, however, access to feral pigs for cultural and recreational purposes could be accomplished with much smaller areas containing free-ranging feral pigs than currently exist (Hess and Jacobi 2014). When considering land designation, the needs of cultural and recreational communities requiring access to feral pig populations must be balanced with conservation efforts resulting from the negative impacts feral pigs have on native ecosystems, and the suite of goods and services that they provide.

Feral pigs can also cause declines in agricultural production and transmit diseases to livestock and humans. The most straightforward aspect of direct impacts on agriculture is crop herbivory; feral pigs may consume excessive amounts of crops, thereby reducing farm production, as demonstrated in Australia (Wurster et al. 2012, Gentle et al. 2015). Feral pigs can also transmit diseases to livestock (Machackova et al. 2003), with diseases of primary concern including African swine fever, classical swine fever, Aujeszky's disease (Gortázar et al. 2007), and bovine tuberculosis (Essey et al. 1983, Machackova et al. 2003, Naranjo et al. 2007). In addition, disease transmission to humans is another important risk to consider with feral pigs, especially for hunters. Previously, feral pigs have been associated with the increased risk of contracting enterococcus in Hawai'i (Dunkell et al., Effects, 2011), Japanese encephalitis virus and brucellosis in Japan (Watarai et al. 2006, Nidaira et al. 2007), hepatitis E virus in Japan and Australia (Meng et al. 2009), trichinella in Papua New Guinea (Owen et al. 2005), and swine influenza virus (Meng et al. 2009).

A case study on the island of Montserrat in the Caribbean revealed that it was five times more economical to manage than to ignore feral pigs because the high level of damage caused to the environment decreased profits in the ecotourism industry (Peh et al. 2015). This is important in the Pacific island region because so many islands are economically dependent on ecotourism.

MANAGEMENT STRATEGIES

The removal of feral pigs and other invasive ungulate species is a well-documented and important step toward effectively improving the habitat of ecosystems damaged by nonnative ungulates (Courchamp et al. 2003). As such, a great deal of time, money, and effort is put into the management of feral pigs each year. Management efforts may use either lethal or nonlethal techniques depending on site-specific goals and resource availability. Overall, the most cost-effective means of managing ecosystems impacted by feral pigs is to address problems directly using an adaptive framework in which researchers test a variety of techniques to determine the most effective way to eliminate feral pigs (Firn et al. 2015, Keiter and Beasley 2017). Recently, technological advances have greatly improved the ability to remotely monitor feral pigs, thereby allowing for more studies of the impacts of various management activities (Engeman et al. 2013).

When lethal removal of feral pigs is selected as the best management option, typically where complete eradication is the management goal, the most frequently used methods include hunting and toxicants (Campbell and Long 2009, Keiter and Beasley 2017). The types of hunting involve snares, sharpshooters, and, frequently in the Pacific, dogs. The challenge with hunting techniques is that, as the number of feral pigs dwindles, the return-on-investment for time spent hunting becomes progressively lower, particularly at population levels <1 pig/km^2 (Anderson and Stone 1993, Barron et al. 2011, Krull et al. 2016). Aerial culling using sharpshooters has shown some success in removing the last remaining pigs from an area (Parkes et al. 2010). However, this method has little utility in densely forested areas, where feral pigs are often found on Pacific islands. Strategies involving both infrared spotting of animals and the use of Judas pigs (released pigs equipped with tracking collars used to lead managers to existing populations) have also been implemented successfully (McIlroy and Gifford 1997, McCann and Garcelon 2008, Melstrom 2014). Comparatively, toxicants used to target invasive mammals in Australia have shown initial population decreases of up to 86% in localized areas (Cowled et al. 2006, Cowled et al. 2007, Campbell et al. 2012). Furthermore, the use of toxicants has been demonstrated as more cost-effective than hunting for feral pig population reduction (Coblentz and Baber 1987, West et al. 2009). As such, it is likely that future feral pig management in the Pacific, where complete removal is the objective, will increasingly rely on toxicants due to the large land areas invaded and difficulty and expense in removing feral pigs via traditional methods. Recently, the U.S. Environmental Protection Agency approved the use of a single warfarin-based toxicant, but the product has yet to be approved for application by any state government.

Many lethal management programs for the removal of feral pigs have the ultimate goal of complete eradication of the species, but this is not true of all programs. Weeks and Packard (2009) showed some success with the management of feral pig populations on private land with hunting in a continental system. Success in controlling feral pig populations via hunting has also been seen in Argentina (Gürtler et al. 2017). However, it is unlikely that this strategy would be feasible throughout most of the Pacific island region due to low numbers of hunters and remote, rugged terrain. As such, eradication is the goal for most programs and is especially common on islands, where the removal of populations can succeed without the fear of natural reintroduction via expansion (Hone and Stone 1989, Parkes et al. 2010).

The one nonlethal management tool that has shown great success in controlling feral pig populations is fencing, which is by far the most common form of nonlethal feral pig management and, perhaps, the most common form and highest expense of land management throughout the Pacific island region. Woven wire fences have been repeatedly shown to be effective in limiting feral pig movement (Giffin 1978, Lavelle et al. 2011). These fences require a minimum height of 1.2 m, because feral pigs can jump over shorter fences (Giffin 1978, Lavelle et al. 2011). Other types of fencing, such as electric fences and mist nets, were shown to be ineffective because feral pigs simply pushed through the mist nets and electrical shocks (Reidy et al. 2008, Lavelle et al. 2011). Once fences are constructed, feral pigs must be completely removed from inside the exclosures. This is almost exclusively completed using the lethal techniques described earlier, particularly hunting. Other nonlethal management techniques for feral pigs have been attempted. However, the use of nonlethal baiting to concentrate feral pigs away from protected areas has proved ineffective (Campbell et al. 2012). In addition, in spite of suggestions that feral pigs' olfactory sense is overlooked in management strategies (Nogueira et al. 2007), the use of odor-based repellants showed no benefit in preventing crop destruction by feral pigs (Schlageter and Haag-Wackernagel 2012).

Although no single method has emerged as a panacea for feral pig control, combinations of both lethal and nonlethal techniques have resulted in cases of successful feral pig eradication. For example, by fencing off large areas into smaller units, personnel at Hawai'i Volcanoes National Park were able to combine the use of snares and hunters with dogs to eradicate pigs from management units on a block-by-block basis (Hone and Stone 1989, Katahira et al. 1993). Another attempt to eradicate pigs from sites on the Hawaiian island of Maui involved using hunters accompanied by dogs to take broad sweeps through fenced areas, which successfully reduced pigs to zero or near zero numbers in all control units (Barron et al. 2011). Eradication from Santa Cruz Island, California, was successful using a multistep process, which started by fencing the island into five zones, trapping for 1,660 trap-nights, shooting feral pigs from helicopters, hunting with dogs, and finally using radio-collared, sterile Judas pigs to track down the final few individuals (Parkes et al. 2010).

PROGNOSIS

Feral pigs have repeatedly been shown to cause a broad range of systematic changes to Pacific ecosystems due to a myriad of cascading direct and indirect effects (Nogueira-Filho et al. 2009) ranging from damage to soils and watersheds (Cuevas et al. 2010, Doupé et al. 2010) to both direct and indirect impacts on endemic flora (Campbell and Long 2009, Cole et al. 2012, Cole and Litton 2014) and fauna (Atkinson and LaPointe 2009). To combat ecosystem degradation from feral pigs, their removal has been established as an effective means for restoring and conserving native ecosystems (Hess 2016).

Despite the clear negative effects of feral pigs on native ecosystems and the positive results seen after their removal, feral pig management in the Pacific island region remains a topic of intense debate. Natural resource managers and government officials largely recognize the damage caused by feral pigs and concentrate resources on their eradication in areas deemed important for the protection of native ecosystems. Alternatively, native cultural practitioners and recreational hunters argue that feral pig populations require management for sustainable harvest as a game species because of the cultural history that surrounds the hunting of feral pigs and their status as a ceremonial food source (Ikagawa 2013). Deepening this debate, an increasing ability to use genetic tests to accurately analyze the ancestry of feral pigs throughout the Pacific has resulted in the argument both for and against eradication based on historical lineages (Linderholm et al. 2016). As a result of these differences in opinion, feral pig eradication occurs almost exclusively on state- and federal-managed lands and other conservation areas so that native ecosystems can be protected without the complete removal of feral pigs from the whole island (Katahira et al. 1993, Ikagawa 2013). In turn, other areas are typically managed for the sustainable harvest of nonnative ungulate populations. Because areas with disparate management objectives related to feral pigs are often found interspersed throughout the landscape, a greater focus on the spatial arrangement of management units holds promise for reducing conflict and the resources required for implementing management activities. Moving forward, expanding the size and number of areas devoid of feral pigs around already existing feral pig–free areas would further protect native ecosystems and the services they provide from the negative effects of feral pigs. For cultural and recreational purposes, smaller populations in more readily accessible areas may be sufficient to support the needs of these individuals while allowing protection of larger areas of native ecosystems throughout the Pacific island region (Hess and Jacobi 2014).

The current body of literature focuses primarily on documenting changes involving alterations to plant communities in the presence of feral pigs. Comparatively, there is a paucity of information regarding the impacts of feral pigs on soils and vertebrate and invertebrate communities. This lack of knowledge includes a need to analyze direct impacts on Pacific avifauna, as well as traditionally overlooked communities of invertebrates. It is also worth noting that the impacts of future climate change on feral pig ecology and distribution have not yet been fully examined (Firn et al. 2015). Feral pig ranges will likely expand northward in continental ecosystems as winters become progressively less harsh (McClure et al. 2015); however, implications are much less clear for island ecosystems that are predicted to be strongly affected by climate change.

ACKNOWLEDGMENTS

We thank R. Laushman for early guidance on the themes of this article and M. Price and two anonymous reviewers for helpful suggestions. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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