Quantifying the impact of wild pigs on global biodiversity and the spatiotemporal ecology of feral pigs on Maui, Hawai'i

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ABSTRACT

Wild pigs (*Sus scrofa*) are one of the most-wide spread terrestrial mammals on the planet and have costly impacts to both natural and managed environments. They were listed as one of the top 100 world's worst invasive species and have caused precipitous population declines and extinctions of some of the most critically endangered species on the planet. Their ability to function as both a top predator and destructive herbivore has made them a particularly serious threat throughout island ecosystems where species are not evolutionarily adapted to defend against such behaviors. In continental ecosystems, they have been shown to fundamentally alter predator-prey dynamics, compete with native fauna, and cause billions of dollars of environmental damage. Given the extensive body of literature documenting these various threats there remain large gaps in our basic understanding of pig ecology and the extent at which they threaten biodiversity. To address these knowledge gaps, this thesis quantified the extent of wild pig threats to 59,590 terrestrial taxa using the largest species data base available: The International Union for the Conservation of Nature's Red List. This thesis also analyzed the spatial ecology of feral pigs on Maui over the spring and fall of 2018 using species distribution models. Results from this thesis indicate that wild pigs threaten 672 taxa world-wide, with plant taxa and herpetofauna (amphibians and reptiles) particularly at risk. Wild pigs threaten nearly as many taxa as domestic dogs and feral cats, who are often regarded by the conservation community as the most problematic invasive species to biodiversity. On Maui, the spatial ecology of feral pigs appeared heavily driven by both temporally variable environmental conditions and differences in hunting pressure. Between the spring and fall of 2018 feral pigs significantly shifted from mixed alien forests into sensitive native mesic shrublands. Management efforts to reduce the significant shift of pig abundance into these sensitive native ecosystems are of the utmost concern.

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CHAPTER 1

Introduction

Wild pigs (*Sus scrofa*) are one of the most problematic terrestrial mammals throughout both their introduced and native range. Intentionally introduced by humans for food provisioning, game recreation, and illegal stocking by hunters, *S. scrofa* now occupy six continents, making them one of the most widely spread terrestrial mammals (Barrios-Garcia and Ballari, 2012). *S. scrofa* are capable of disturbing ecosystems through a suite of mechanisms that influence both top-down and bottom-up regulatory pressures, including: the depredation of herpetofauna in Alabama and Georgia (Jolley et al., 2010), disturbing predator-prey dynamics in the Channel Islands (Roemer et al., 2001), altering soil conditions in Hawai'i (Long et al., 2017; Wehr, 2018), and decreasing plant species richness in Australia (Hone, 2002). Wild pigs cause billions of dollars a year in damages in the United States alone and the geographic distribution of pig populations is expected to expand with changes in climate (McClure et al., 2015; Pimental, 2007).

To address the magnitude of impacts to the environment from wild pigs and their expanding geographic distribution, the National Wild Pig Task Force (NWPTF) set forth research priorities to address knowledge gaps in wild pig biology and ecology, economic and ecological effects, control strategies, and education and human dimensions (Beasley et al., 2018). Chapters 2 and 3 of this thesis aim to address some of the most pressing research priorities as set forth by the NWPTF to better understand the extent of wild pig impacts to biodiversity and their basic ecological requirements.

Chapter 2 of this thesis aims to quantify the global ecological effects of wild pigs on biodiviersity. The NWPTF explicitly call for a better understanding of the impacts of wild pigs on natural environments, as these are much less understood and studied than their impacts on managed ecosystems (e.g., agriculture) (Beasley et al., 2018). This study aims to address that knowledge gap and is the first to quantify the extent of wild pig impact based on all their known mechanisms of disturbance throughout their native and introduced range. This global quantitative study helps identify both taxonomic groups and regions most threatened by wild pigs, thereby directing conservation and management attention to vulnerable taxa and regions.

Chapter 3 of this thesis addresses the basic spatiotemporal ecology of feral pigs on the second largest Hawaiian Island. It is important to note here that wild populations of pigs in Hawaiʻi are referred to as feral due to their genealogy indicating the Hawaiian breed to be a genetic hybrid of domestic, feral, and wild populations of swine (Cheong H. Diong, 1982; Wehr et al., 2018). Although both feral and wild pigs are classified as the same species (*Sus scrofa*), Chapter 3 of this thesis refers to Hawaiian populations of pigs as feral while Chapter 2 generally refers to wild pigs throughout their native and introduced range (treating feral pigs as introduced populations of wild pigs). Overall, very little is known about which biotic or abiotic factors drive feral pig densities in Hawaiʻi, and even less is known about how temporal fluctuations in those factors influence their distribution. The island of Maui provides an ideal system for studying the distribution of feral pigs because of the diverse array of habitat types, relatively small size when compared to continental systems, and well-established feral pig populations. Through spatial modeling techniques, this study identifies primary drivers of feral pig distribution between two contrasting seasons and quantifies the change in feral pig distribution. On a more basic level, this study provides reproducible, cost-effective methods for quantifying feral pig abundances that are

explicitly called for by the NWPTF. The results from this study have broad-reaching applications particularly for management agencies in Hawai'i, where an understanding of feral pig distribution may mitigate potential conflict between conservation and game management objectives.

CHAPTER 2

Quantifying the impact of wild pigs on global biodiversity

Abstract

Humans have facilitated the spread of species outside of their native ranges into regions where they did not historically occur, leading to significant impacts to native biodiversity on a global scale. The modes of distribution and establishment of exotic and invasive species are well studied and documented, but the degree of impact of invasive species on biodiversity is difficult to enumerate. The IUCN Red List is a comprehensive list of over 105,700 species and is a powerful tool to quantify the threat of problematic species. In this chapter, I aim to quantify the impacts of a globally distributed invasive species, wild pig (*Sus scrofa*), that is known to modify ecosystems through predation, disturbance and degradation of habitat, disease risk, competition, and hybridization. In total, 672 taxa were recognized as threatened by wild pigs throughout 54 different countries. Out of the 672 taxa, 414 were either endangered or critically endangered species and 14 species listed *Sus scrofa* as a major contributing factor to their extinction. Additionally, island ecosystems were found to be more vulnerable to threats from *Sus scrofa*, a phenomenon particularly driven by species of concern on islands throughout Polynesia, Micronesia, and Melanesia. Wild pigs ranked among some of the most problematic invasive predators such as feral cats and domestic dogs. Threatened species were distributed across taxonomic groups indicating pervasive ecosystem level threats, however, island plants and herpetofauna were among the most threatened taxa.

Introduction

Wild pigs (*Sus scrofa*) originate from Eurasia and were first domesticated around 9000 years ago (Larson et al., 2005). Since domestication, humans have brought pigs to nearly every corner of the globe where feral populations have quickly established. Their utility as a food provisioning resource has made pigs one of the most widely distributed mammals in the world and inevitably led them to regions previously unexposed to large terrestrial omnivores (Massei and Genov, 2004). Most commonly island ecosystems, these unexposed regions are particularly vulnerable to the presence of invasive species due to native and endemic species lacking appropriate evolutionary and behavioral traits (Banks and Dickman, 2007; Gibbons et al., 2000; Parker et al., 2006).

Pigs were listed in "100 of the World's Worst Invasive Alien Species" solidifying their spot amongst other more frequently discussed invasive terrestrial species such as feral cats (*Felis catus*) and rats (*Rattus rattus*) (Lowe et al., 2000). Pigs are unique among other problematic terrestrial invasive species; in that they are omnivorous generalists and function as both large predators and herbivores throughout their native and introduced range (Barrios-Garcia and Ballari, 2012). They have been documented predating upon a variety of vertebrate and invertebrate species throughout island and continental ecosystems (Challies, 1975; Coblentz and Baber, 1987; Jolley et al., 2010), disturbing nest sites and plant assemblages (Cole and Litton, 2014; MacFarland et al., 1974), hybridizing with other endangered Suidae (Semiadi and Meijaard, 2006), competing with native fauna (Desbiez et al., 2009; Focardi et al., 2000), and as vectors for disease transmission (Barrios-Garcia and Ballari, 2012; Gortázar et al., 2007; Spear and Chown, 2009). In addition to their direct impacts on both wildlife and plant communities, they are generally known to disturb ecosystem structure due to their unique rooting and digging

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behavior (Mitchell et al., 2008). Consequentially, pigs are considered ecosystem engineers, having considerable secondary effects on organisms by physically altering habitat characteristics (Barrios-Garcia and Ballari, 2012). To accurately address the extent of pig threats to biodiversity these various threatening mechanisms (predation, herbivory, and ecosystem engineering) must be incorporated in any comprehensive threat assessment.

Although global summaries of pig impacts do exist they have either been global qualitative papers drawing implications from many small-scale quantitative studies (Ballari and Barrios-García, 2014; Barrios-Garcia and Ballari, 2012; Massei and Genov, 2004; Nuñez et al., 2010; Spear and Chown, 2009) or have been large-scale quantitative studies addressing a specific mechanism through which pigs threaten the environment (Bracke, 2011; Doherty et al., 2016) or their impacts on a particular ecosystem type (Campbell and Long, 2009). Global qualitative review papers are critical in identifying the mechanisms and effects pigs have on ecosystems yet are insufficient in quantifying the extent of these impacts to species and environments outside of the areas from which the data is drawn. Furthermore, large-scale quantitative papers are rare and typically focus on one aspect of species impact (predation, herbivory, or ecosystem engineering). As a result, a comprehensive global quantitative assessment including all mechanisms through which pigs threaten biodiversity is nonexistent.

In this chapter, I quantify the extent of pig threats to both plant and wildlife including all mechanisms by which pigs threaten these taxa and all potentially threatened taxa. Using this information, I enumerate how many species are threatened by pigs and which taxonomic groups are most vulnerable. I also identify which threatening mechanisms are most prevalent and which regions globally can be considered hotspots in terms of pig threats.

Methods

A complete copy of the IUCN Red List for all terrestrial vertebrates was acquired in June 2018 (*n*=67,246 taxa). Data deficient taxa were excluded from this database due to uncertainties surrounding their assessment accuracy. The refined database (*n*=59,590 taxa) was then filtered using a systemic search in R (R Core Team, 2013) to identify keywords from the "Major Threats" section for each species that contained any of the following keywords: pig, pig*, pigs, domesticus, Sus, scrofa, boar, boar*, boars, hog, hog*, hogs, swine. This list of keywords was compiled based on commonly used names to describe pigs in management literature. This script flagged a total of 815 taxa for manual review. I did not include threats associated with domesticated pigs, however, domestic pigs described as "free-ranging" were treated as wild. Similarly, some species were not threatened by pigs directly, but instead by human hunting practices catalyzed by the presence of pigs. These threats were noted but not included in the analysis. False positives were flagged and removed from the pig threatened species subset.

The "Major Threats" section was then manually read and cross referenced for a final set of 672 taxa. To ascertain the threat level from wild pigs to these taxa I used a similar approach to previous studies and categorized threat level as "major", "minor", or "potential" based on information provided in the "Major Threats" section and the taxa's current threat status (Doherty et al., 2016; Jones et al., 2008; Medina et al., 2011). I chose to include "potential" instead of "mixed" like many other studies due to uncertainty surrounding some of the threat text associated with the threatened taxa. Threats from wild pigs were sometimes inferred by the listing's author based on overlapping distribution of the threatened species with wild pigs but evidence of direct impact was sometimes missing. In these cases, threats from wild pigs were categorized as "potential". When threats were associated with extinct or critically endangered

taxa, text alluding to any threat from wild pigs were considered "major". Threats to least concern taxa were considered by default to be minor as were secondary threats to near-threatened taxa unless otherwise specified. For each taxon threatened by pigs, I categorized threat as one or more of the following categories: "predation", "disturbance", "disease risk", "competition", and "hybridization". Unless otherwise specified, consumption of plants by wild pigs was considered both "predation" and "disturbance". Similarly, digging up of nests of herpetofauna and ground nesting birds was counted as both "disturbance" and "predation".

Range information obtained from the IUCN Red List was categorized into 18 different sub-regions (Fig. 2.1). These sub-regions were additionally classified as either island or continental based on their geographic location for a comparative threat analysis. Since IUCN Red List range data is classified by country, many endemic species occurring on islands were cross listed as occurring on both the country which governs the island and the island on which they were present (n_0 = 3017). These cross-listings would have overinflated the threats occurring in continental regions. Using the built-in filter functions in Microsoft Excel and more detailed range information from the "Range Description" text from the IUCN Red List, each of the 3017 taxa were manually filtered by reading each taxa's range information and repeat records of endemic species outside of their range were removed (n_1 = 2496).

Results

Global threat from wild pigs on biodiversity

Wild pigs were documented as a threat to 672 species from 54 different countries. Of these, 267 taxa were classified as critically endangered, 147 taxa were endangered, and 14 extinct taxa had classified pigs as a major contributing factor to their decline (Fig. 2.2 & Fig.

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2.4). Disturbance of habitat threatened 594 taxa making it the most frequently cited threat type, followed by 486 taxa threatened by predation with all other threat types affecting less than 20 taxa (Fig. 2.3). Of the 672 taxa threatened by pigs, 345 were plants (59 families), 123 herpetofauna (25 families), 96 birds (38 families), 84 invertebrates (22 families), and 24 mammals (11 families) (Fig. 2.2). In total, 59% of threatened taxa faced major threats, 21% faced minor threats, and 20% were potentially threatened by wild pigs (Fig. 2.4). Nearly a third (30%) of all threatened taxa facing major threats were distributed amongst three plant families (56 *Campanulaceae*, 26 *Asteraceae*, and 21 *Arecaeae*) and one reptile family (24 *Scincidae*).

3.2. Continental vs. Island Regions

Wild pigs in island regions generally have stronger negative impacts on biodiversity when compared to continental regions (Fig. 2.5). Plants and herpetofauna were the most threatened island taxa while birds and herpetofauna were the most threatened continental taxa (Fig. 2.5). Collectively, the Micronesian/Melanesian region had the highest severity of assessed taxa threatened by wild pigs including 19% of all invertebrates (64 taxa), 13% of herpetofauna (67 taxa), 4% of plants (59 taxa), and 2% of all birds (25 taxa). The Polynesian islands were the next most threatened island region with 31% of plants (248 taxa) threatened, 14% of herpetofauna (5 taxa), and 9% of birds (31 taxa). Notably, 18% (9 taxa) of all assessed herpetofauna in the Galapagos were threatened by wild pigs with over half of them belonging to the *Testudinidae* family. For continental regions, North America faced the highest threat rates from wild pigs with 1% of all birds (11 taxa), 0.9% of reptiles (5 taxa), and 0.5% of mammals (2 taxa).
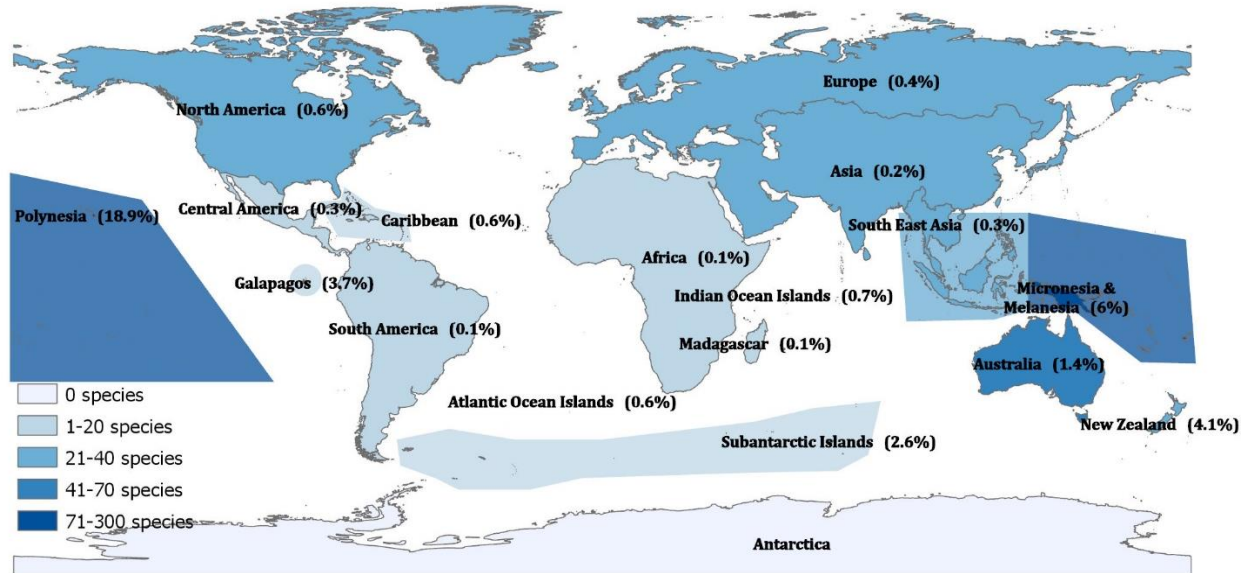
Fig. 2.1. Number of taxa threatened by wild pigs for each of the 18 subregions. Percent of all assessed taxa threatened are given in parenthesis. Antarctica was the only subregion without wild pig presence therefore (%) not given.

Table 2.1. List of species with wild pigs classified as a major contributing factor to their extinction.

Common Name	Species Name	Region
-	*Melicope nealae*	Hawai'i
Kauaʻi flatsedge	*Cyperus rockii*	Hawai'i
-	*Cyanea sessilifolia*	Hawai'i
Tristan moorhen	*Gallinula nesiotis*	Saint Helena
South Island snipe	*Coenocorypha iredalei*	New Zealand
Kauaʻi ʻōʻō	*Moho braccatus*	Hawai'i
Hawaiian Greensword	*Argyroxiphium virescens*	Hawai'i
-	*Hibiscadelphus woodii*	Hawai'i
-	*Delissea niihauensis*	Hawai'i
-	*Melicope macropus*	Hawai'i
Mt. Kaala cyanea	*Cyanea superba* ssp. *regina*	Hawai'i
Mount Glorious day frog	*Taudactylus diurnus*	Australia
-	*Chilonopsis nonpareil*	Saint Helena
-	*Tetramolopium consanguineum* subsp. *consanguineum*	Hawai'i

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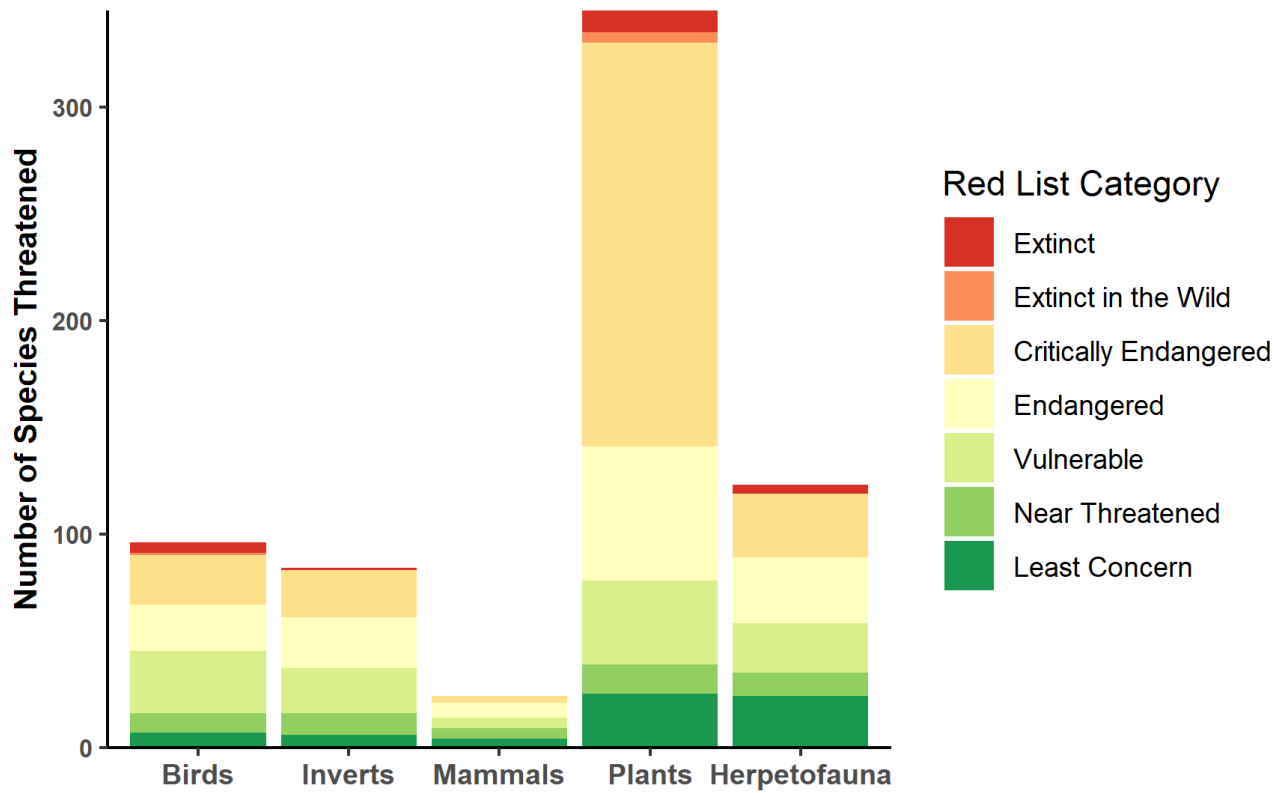
Fig 2.2. Wild pig threats to each taxonomic group categorized by their Red List Category.
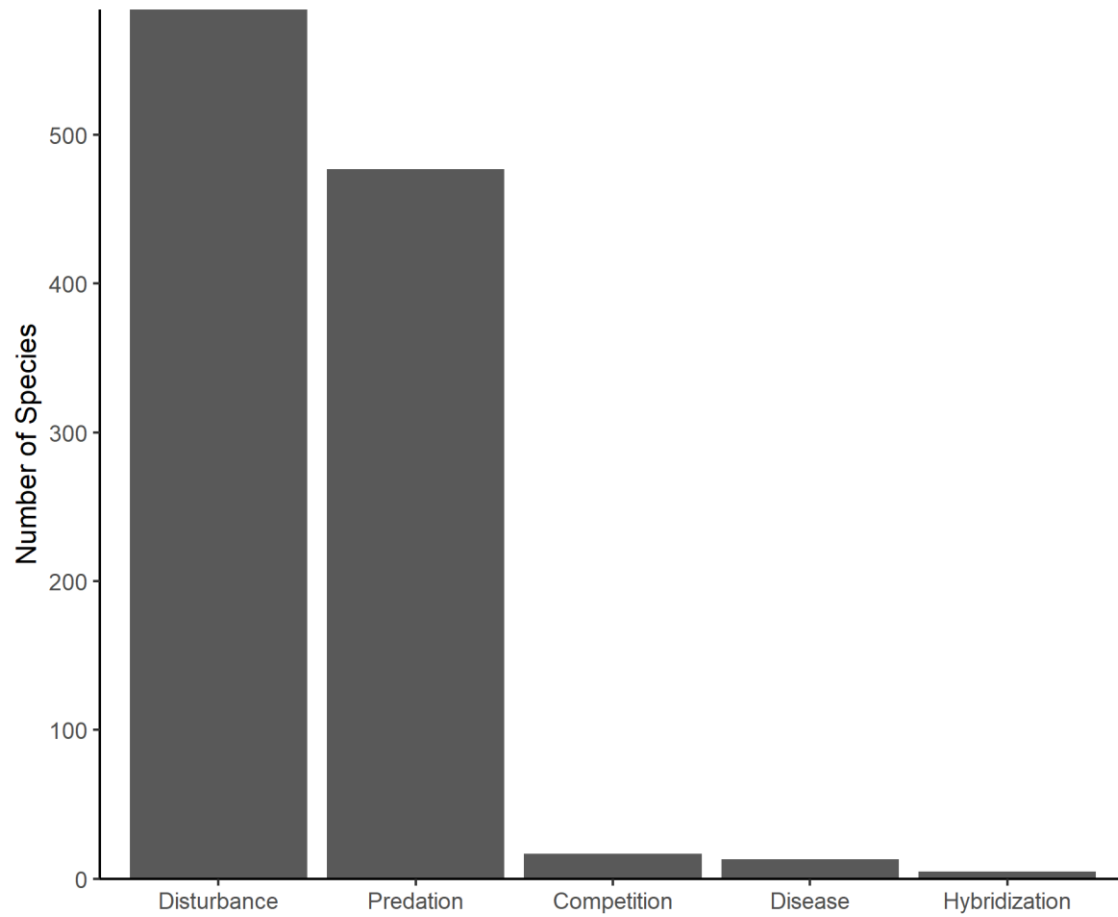
Fig 2.3. Frequency of wild pig threat types to all IUCN assessed species as described in the "Major Threats" category.
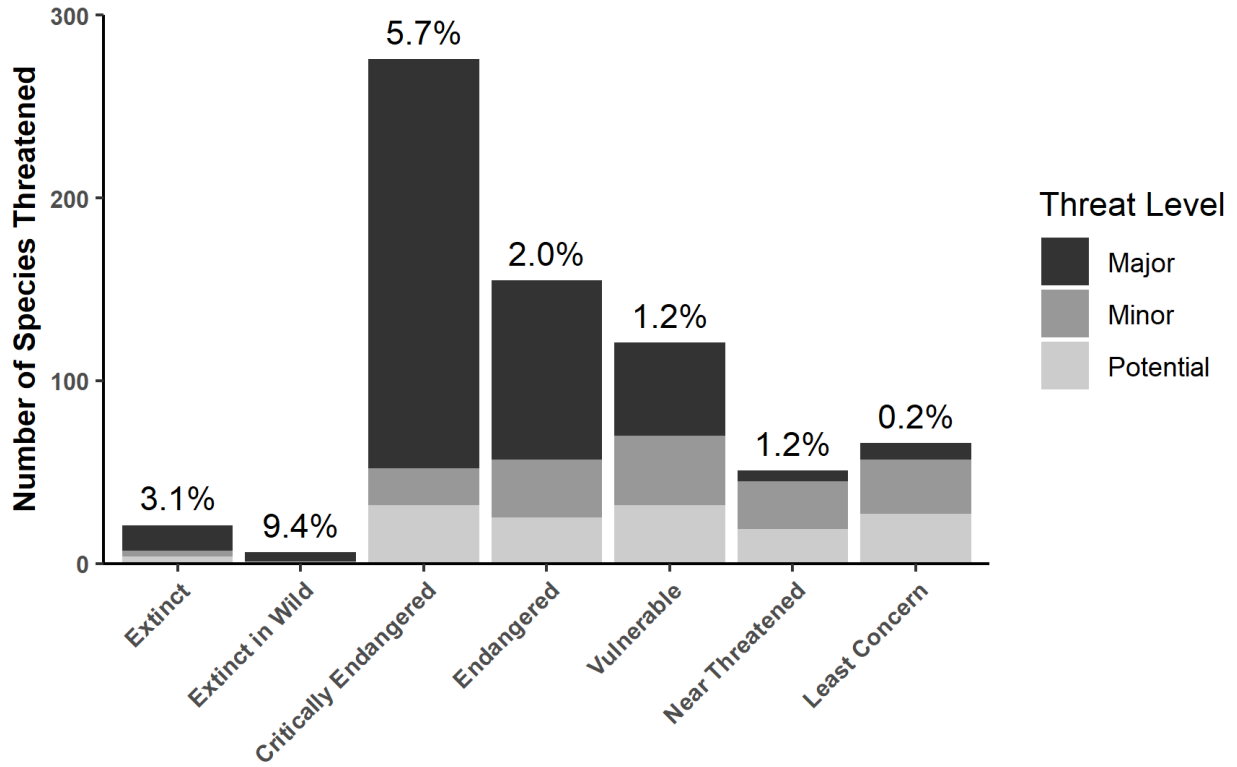
Fig 2.4. Severity of threats to taxa based on their Red List Category with percentage (%) of total species listed labeled on top of bars.
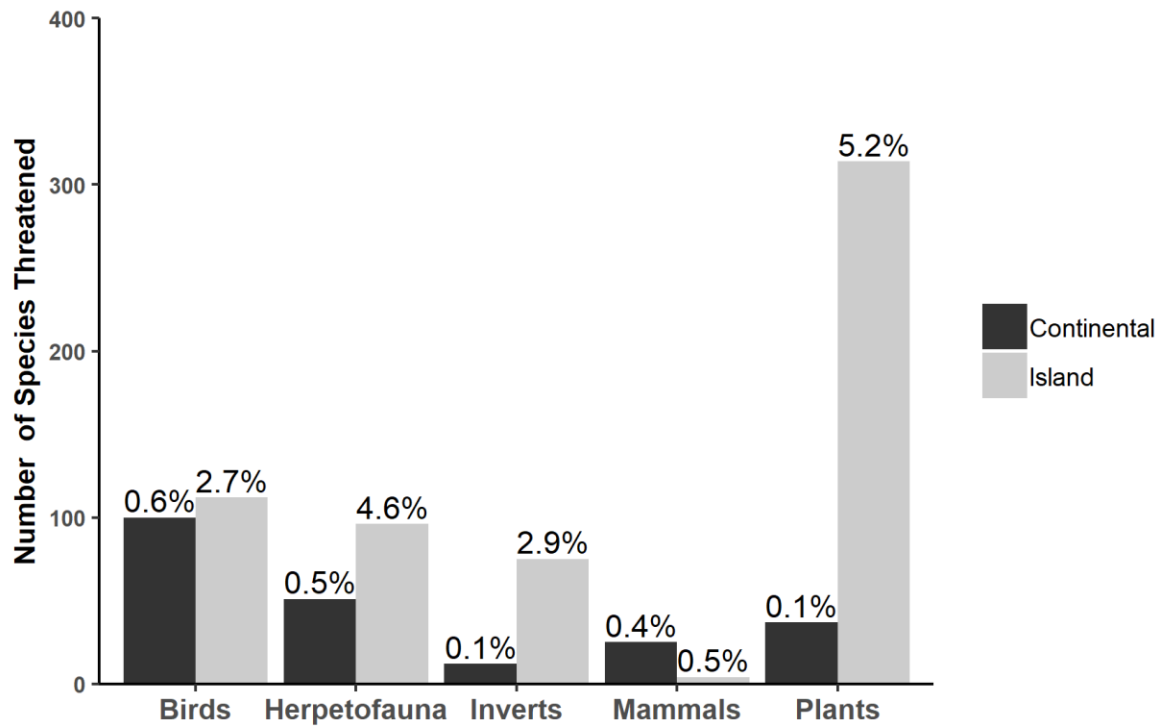
Fig 2.5. Number of species threatened by wild pigs on continental and island ecosystems with proportion of species (%) displayed above columns.

Discussion

This study is the first comprehensive analysis to quantify the threat to global biodiversity from wild pigs in both continental and island ecosystems. This assessment indicates that wild pigs are non-discriminant generalists, threatening 672 taxa globally, and have contributed to the extinctions of 14 taxa. I also reiterate that over half (*n*= 414 taxa) all taxa threatened are listed as either critically endangered or endangered and are of the greatest conservation concern. The estimates from this assessment are likely conservative due to the exclusion of data deficient species in the analysis and known biases associated with threat reporting and species assessments (Bland et al., 2015; Böhm et al., 2013; Keith et al., 2015). Furthermore, wild pigs have highly destructive behaviors that cause cascading trophic effects which broadly impact ecosystems, yet these threats are not easily quantified and most likely are largely excluded from species assessments (Barrios-Garcia and Ballari, 2012; Massei and Genov, 2004; Roemer et al., 2001). Although excluded from this analysis, I also found frequent mention of bycatch by hunters alluding to further impact associated with the presence of wild pigs.

Impacts to islands from wild pigs are particularly acute, especially in the Polynesian region. This result is overwhelmingly driven by taxa in the Hawaiian Islands; with 92% of all taxa threatened by pigs in this region occurring on the Hawaiian Islands. This is likely due to data deficiencies in species assessments on smaller developing island countries throughout Polynesia (Brummitt et al., 2015). Studies have found that these data deficient species are typically of high conservation concern and our results may imply that threats to taxa throughout these data deficient areas of Polynesia may be comparable to those faced by taxa in the Hawaiian Islands due to similarities in ecosystem structure (Bland et al., 2015; Joppa et al., 2011). Thus,

the threats to the broader Polynesian region as well as other data deficient regions around the world may be considerably greater than indicated.

Proportionately, island plants and herpetofauna are the most threatened species. Herpetofauna are threatened by both direct predation and disturbance to nest sites. Herpetofauna in the Galapagos and Micronesian/Melanesian region were found to suffer higher threat rates than elsewhere (18% and 13% respectively). For island regions with insufficient species assessments, this is particularly important as herpetofauna present there may be more threatened by wild pigs than indicated by this assessment. More comprehensive species assessments and research attention to island herpetofauna is needed as they are one of the most data deficient taxonomic groups on the Red List (Bland and Böhm, 2016; Jones et al., 2016; Stuart et al., 2004). Generally, plants had the highest number of taxa threatened by pigs, with this result driven by species in Polynesia (n = 248 taxa) or Micronesia/Melanesia (n = 58 taxa). Island native and endemic plants are most likely threatened in these regions due to the absence of analogous terrestrial mammalian omnivores throughout their evolutionary history (Denslow, 2003). As a result, many island plant species lack the evolutionary traits and behaviors that can protect them against omnivorous ungulates (Desurmont et al., 2011; Parker et al., 2006). The same is likely true for island herpetofauna, leaving them naïve to threats from wild pigs (Banks and Dickman, 2007; Courchamp et al., 2003; Cox and Lima, 2006).

This analysis suggests nearly five times more taxa are threatened by wild pigs than an IUCN meta-analysis conducted by Doherty et al. (2016). Incorporating both plants and amphibians which were excluded from Doherty et al. (2016) and rank among the highest threatened taxa, is crucial in identifying the true extent of wild pig impact to biodiversity due to their non-discriminant nature. The keyword search in this assessment also included a wider range

of search terms due to preliminary research and consultation with IUCN indicating a wide range of terms used to describe *Sus scrofa*. Even so, the list of species impacted by pigs is likely an underestimate, as plants, invertebrates and herpetofauna are often data deficient, or have not been assessed by the Red list (Bland and Böhm, 2016; Howard and Bickford, 2014). Additionally, pigs have often been present in many island ecosystem (where they have the greatest impact) for a longer period than other predators (e.g. cats or dogs) meaning that historical declines caused by the introduction of pigs may be poorly documented.

The threats from wild pigs rank among many of the most problematic invasive predators that have undergone similar analyses (Doherty et al., 2016, 2017; Medina et al., 2011). Many of these assessments exclude threats to terrestrial invertebrates and plants as well as any threats to species of least concern or near threatened status. If both these criteria were excluded from our assessment wild pigs still threaten 183 taxa globally (80 birds, 15 mammals, 88 reptiles) ranking them among some of the world's top invasive predators such as domestic dogs (Doherty et al., 2017). Also, threats to island regions from wild pigs rank closely to feral cats (*Felis catus*), which are often regarded as the most detrimental invasive predator to island ecosystems (Nogales et al., 2013). Medina et al. (2011) identified 175 taxa threated by feral cats on islands, while our assessment indicates wild pigs threaten at least 147 taxa using the same criteria. Given the role of wild pigs as both a top predator and destructive herbivore, their additional threats to plant and invertebrate taxa make them a serious cause for concern and indicate major ecosystem level impacts (Simberloff, 2011). Furthermore, wild pigs not only threaten a comparable number of taxa as other invasive predators, they impact taxonomic groups that are often minimally threatened by other invasive species, such as herpetofauna and plants (Bellard C. et al., 2016).

Given these extensive threats, there are multiple ways to effectively manage for pig threats on both island and continental systems. In many cases, wild pigs are an abatable threat, with available management actions like exclusion fencing, baiting, trapping, and eradication on smaller islands or from protected areas (Courchamp et al., 2003). Island regions, which are most threatened by the presence of wild pigs, have benefited from successful eradication campaigns and the subsequent recovery of native species across taxonomic groups are indicative of major ecosystem level impacts associated with their presence (Brooke et al., 2007). Eradication efforts have even been successful for larger islands (>100km^2) where threatened endemic species are beginning to recover (Coblentz and Baber, 1987; Cruz et al., 2005; Ramsey et al., 2009). Although quantitative information on native species recovery after eradication is uncommon, Donlan et al. (2007) found considerable increases in the density of the endemic Galapagos rail (*Laterallus spilonotus*) after goat and pig eradication. Where eradication is not feasible (densely populated islands or continental regions), other adaptive management approaches in the form of targeted control efforts (Gürtler et al., 2017; Weeks and Packard, 2009) and protected refuges using exclusion fencing have helped alleviate pig pressures on vulnerable taxa (Cole and Litton, 2014; Lavelle et al., 2011). However, given these management options the amount of conservation effort dedicated toward wild pig management on islands is disproportionate to the threats they face as evidenced by this assessment (Jones et al., 2016). Few islands include comprehensive pig management for the purposes of conservation and only 69 islands have been eradicated of wild pigs (DIISE, 2018). In comparison, 148 islands have been successfully eradicated of cats (*Felis catus)* and 195 have been eradicated of feral goats (*Capra hircus)* (DIISE, 2018). This assessment suggests that pig control efforts on island ecosystems would have the greatest benefit to biodiversity, particularly throughout Polynesia, Micronesia, and

Melanesia. Additionally, special concern should be placed on islands with a diverse presence of herpetofauna or native plant species due to their vulnerability. Finally, more research attention should be focused on island herpetofauna as they are typically data deficient and threats to these taxa are likely far greater than indicated by this assessment.

CHAPTER 3

Spatiotemporal ecology of feral pigs on Maui, Hawai'i

Abstract

Species distribution models (SDM) are commonly used in resource planning to prioritize management decisions but temporal variation is often excluded from the modeling process. As a result, few studies appropriately incorporate the influence of temporal variation on species distribution, potentially biasing management recommendations based on SDM outputs. In this chapter, I aimed to address how temporal variation in environmental and human-mediated conditions might affect the modeling of the distribution of a large omnivorous ungulate on the second largest main Hawaiian Island. Abundance data obtained from remote camera traps and systematic disturbance surveys were rigorously collected over the fall and spring periods of 2018, providing high resolution species data to be used as inputs for an SDM. Using multiple modeling methods and quantitative analysis on model outputs I found significant variation between models of feral pig distribution produced from these two seasons of data collection. Furthermore, I found that foraging behavior likely shifted between the fall and spring. Feral pigs appeared to prefer mixed alien forests from March to May of 2018 (spring) but shifted to open native mesic shrublands from October to December 2018 (fall). Finally, I found that mixed alien forests in Hawai'i host abundant feral pig populations, compared to other habitat types and islands, and more management attention should be placed on these areas as they may play a critical role in increasing feral pig disturbance on surrounding sensitive native ecosystems.

Introduction

  Species distribution modeling (SDM) is an increasingly common approach to addressing complicated conservation and game management issues that deal with a spatially heterogenous species (Froese et al., 2017; McClure et al., 2015). By modeling the distribution of that species, management agencies are then able to prioritize management decisions based on the species distribution and abundance. For conservation agencies, modeling the distribution of an invasive species enables them to identify hotspot biodiversity areas that might be most threatened by that invasive species (Tulloch et al., 2015). For game management agencies, an SDM of a valuable game mammal allows managers to prioritize which areas might be most productive for hunting. By selectively identifying areas with low native biodiversity but high non-native game mammal abundance, managers may achieve game management objectives while minimizing conflict with conservation management objectives.

  However, SDM is complicated by the influence of seasonal variation in both environmental and human mediated conditions that alter the spatial ecology of the species of interest. Feral pigs commonly change their spatial ecology and foraging behavior in the continental United States and Europe in response to seasonal variations in climate (Amendolia et al., 2019; McClure et al., 2015; Morelle and Lejeune, 2015). The ability to adapt to fluctuating conditions by shifting their distribution seasonally complicates the SDM approach by introducing a temporal component into a spatially explicit model. Furthermore, human mediated interactions with feral pigs, such as hunters or hikers, have significant effects on habitat selection (Merli et al., 2017; Mysterud and Østbye, 1999). Variation in the frequency and quantity of hikers and hunters in an area throughout the year will likely influence the distribution of feral pigs. The influence of these temporally variable factors on the spatial ecology of feral pigs are

rarely studied but are essential to understanding where pigs are moving throughout the year and which conditions are primary drivers of that movement (Beasley et al., 2018). To appropriately align management actions with conservation and game management objectives, a basic understanding of temporal differences in feral pig distribution is essential.

The island of Maui, Hawai'i provides an ideal system for studying the spatiotemporal ecology of feral pigs. Feral pig populations have been established on Maui for atleast several hundred years meaning they have likely realized their available niche space (Cheong H. Diong, 1982). The island of Maui has a diverse array of habitat types present in both island and continental systems, making comprehensive field studies feasible and results potentially applicable to continental systems. Environmental conditions are spatially and temporally variable with a distinct wet and dry season. Finally, applications of species distribution modeling for two objectives, conservation and game management, are relevant in Hawai'i as feral pigs are managed as both a destructive invasive pest and an important cultural and recreational resource. Maui therefore provides an opportunity to test the effects of seasonal changes in environmental conditions on feral pig spatial ecology and allows for the subsequent application of species distribution modeling results in both a conservation and game management context.

This chapter aims to compare the spatial ecology of feral pigs between two contrasting seasons, spring 2018 and fall 2018, on Maui, Hawai'i and identify primary drivers influencing the potential change in distribution using the most common approaches to species distribution modeling. I hypothesized that seasonality would significantly affect the distribution of feral pigs due to changes in the frequency and quantity of rainfall, changes in temperature, and differences in hunting pressure. During the drier spring season, I expected that pig distribution would be constrained to areas that provided cover from hunting pressure and sources of food during

months of lower rainfall. During the wetter fall season, I hypothesized that pigs would be less

reliant upon these forested areas that provide cover and the closure of many hunting units would

alter feral pig foraging behavior and habitat selection. I expected this change in foraging

behavior to result in a significant shift in feral pig distribution between seasons.
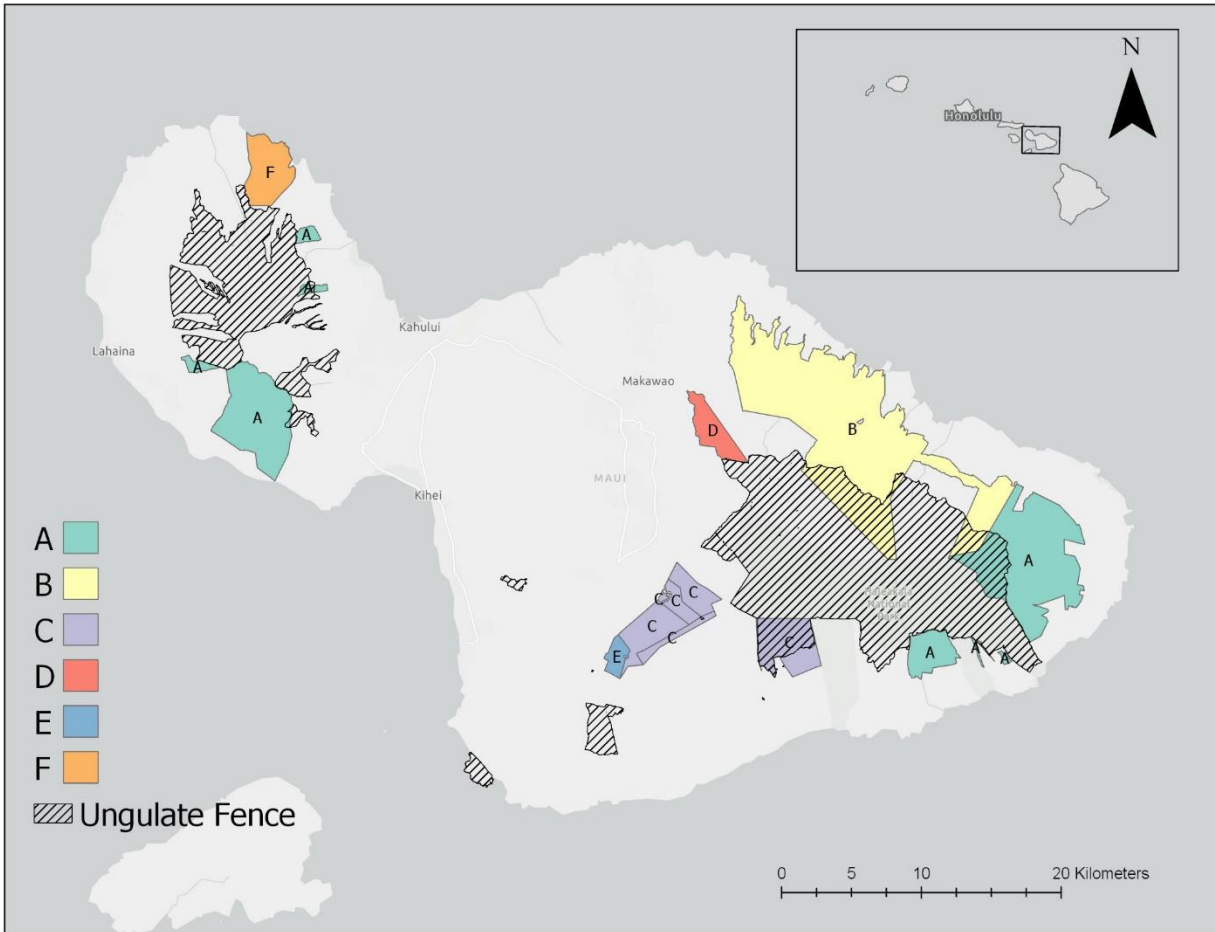
Fig. 3.1. Hunting units across the island of Maui denoted by the type of unit and existing ungulate fences represented by hatched lines. Deer and feral pigs are eligible for take from all hunting units. Goats are eligible for take from units A, B, C, and D while hunting units E and F are exclusively for feral pigs and deer. Units A, B, D, and E are open to feral pig hunting year-round. Unit C is open to feral pig hunting from February through June and Unit F is open to feral pig hunting from February through October.

Site Description

The island of Maui is the second largest Hawaiian Island and has a land area of 1883 km^2 (Fig. 3.1). There are two main mountain ranges, the West Maui mountains with elevations up to 1,764 m and East Maui mountains (Haleakalā) with elevations up to 3,055 m. The East Maui mountains were created through volcanic activity that began around 840,000 years ago and remained active until as recently as 1790 (Sinton, 1979). East Maui is a shield volcano characterized by its gradual sprawling slopes due to limited exposure to erosion in geologic time. The West Maui mountains were created through several volcanic series that began at least 1.2 million years ago and subsided around 500,000 years ago (Sinton, 1979). In contrast to East Maui, West Maui has been exposed to erosive weathering for nearly 400,000 years longer, resulting in steep topography that is generally inaccessible by foot. Long-term mean annual rainfall varies greatly across the island from 250 mm to over 10,000 mm (Giambelluca et al., 2012). The north-eastern face of Haleakalā receives the greatest amount of rainfall due to the predominant northeasterly trade winds.

Public hunting areas comprise nearly 15% of Maui's land area (275 km^2) with various restrictions on hunting seasons, daily bag limits, and sex of species eligible for take. Ungulate fencing is the most common approach for minimizing impacts from invasive ungulates to native species and ecosystems on the island of Maui and across most of the state of Hawai'i. There are 231 km of existing ungulate fences on Maui and they are present in both mountain ranges. However, due to differences in terrain, approaches to ungulate fencing differ between East and West Maui. West Maui ungulate fences are strategically constructed to prevent movement of ungulates through critical corridors, with cliff areas unfenced, effectively preventing ungulates

from accessing higher elevations. Ungulate fences on East Maui are designed with a single continuous fence encompassing the East Maui mountains.

Hunting seasons generally play an important role in the distribution of game species and the accessibility of optimal foraging habitat (Stankowich, 2008). As such, it is important to consider not only the landscape of biotic and abiotic variables but also the landscape of human interaction with the environment, most notably the presence or absence of hunting pressure. During spring 2018, all hunting units were open for game mammals with limited hunting access during fall (Fig 3.1)

Methods

Seasonal conditions:

Long-term average climate data were obtained from the rainfall atlas of Hawaiʻi's website and were used as expected climatic conditions for each season of data collection. These long-term averages were then cross-referenced with observed data from local weather stations to characterize 2018 field conditions. Observed weather station data were obtained from Remote Automated Weather Stations (RAWS) and the National Oceanic and Atmospheric Administration's (NOAA) National Weather Service. Weather station locations included Kahului, Kula, and Keālia National Wildlife Refuge.

Site selection:

Potential survey sites were located by rasterizing the island of Maui into 500 by 500 meter (25 ha) units using R packages raster (Hijmans et al., 2017) and rgdal (Bivand et al.,

2018). Sites were located at the centroid of each raster cell. The raster was masked to land

recognized as a forest reserve using the Hawai'i state government reserve outline (State of

Hawai'i 2016) and privately held land with pre-established access permission. For this reason,

extensive areas of fallow agricultural land and urban areas were not sampled. Additionally, all

land within ungulate exclusion fences was excluded from the random site selection process, since

ungulates have been excluded and eradicated from these locations. To ensure sampling across

altitudinally stratified environmental gradients which commonly occur in the Hawaiian Islands,

potential survey areas were divided equally into three altitudinal bands (0-1000 m, 1000-2000 m

and >2000 m) to prevent disproportionate sampling of the more frequent, low altitude raster

cells. An equal number ($n=15$ per band) of survey sites was randomly drawn from these three

altitudinal bands. Randomly stratified sites were generated for both the spring and fall seasons of

data collection. The vegetation, slope, and topography of Hawaiian habitats make it difficult to

both access sites and deploy camera traps. When a randomly selected site could not be reached

due to topography, the site was moved to the closest analogous location within 500m that could

be safely accessed, or else was excluded from the study. Sites requiring helicopter were accessed

via the nearest accessible landing zone (LZ). If sites could not be reached via LZ, camera traps

and surveys were deployed in a rectangular array on an azimuth towards the site location no

greater than 500 m from the site location.
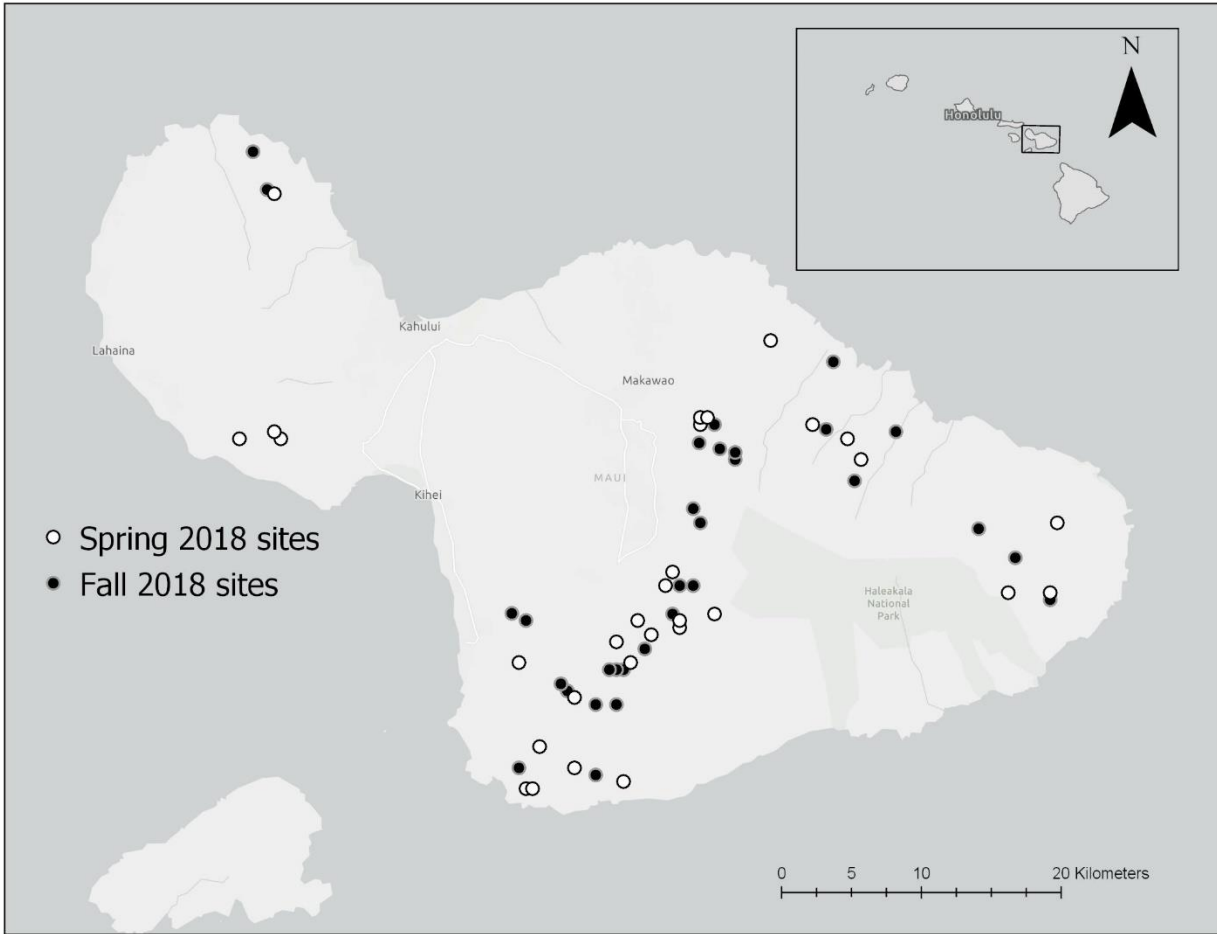
Fig. 3.2. Map of Maui, Hawaiʻi showing site locations for both spring and fall data collection where camera traps were deployed, and disturbance surveys were conducted.

Survey design:

At each site an array of six cameras was installed (Bushnell Trophy Cams) distributed at regular 50 m intervals (Bushnell Trophy Cams, Bushnell, Overland Park, KS). Cameras were programmed to take two consecutive images for each trigger and reset after three seconds. Sites were deployed for a two-week period under one of two configurations depending on terrain: (i) a rectangular array, with cameras deployed in two parallel lines of three; and (ii) a linear array, with all six cameras deployed along a transect. Linear arrays were deployed only in areas where topography did not allow for a rectangular array, such as on ridge crests with steep receding slopes on either side. Cameras were deployed in a manner that maximized the probability of

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detection, such as focused in a clearing, trail or area with obvious previous pig activity within a 10 m radius of randomly pre-selected GPS co-ordinates. Cameras were attached to vegetation at approximately waist height and angled on a level to slightly downward facing trajectory with the ground. Camera data were reviewed manually using Irfanview (version 4.53) so that photos containing images of feral pigs were filtered into a database for analysis (Škiljan, 2019). After filtering, the mean count of camera-captured observations of feral pigs per site was calculated and used as one form of count data for model building.

At each camera location, signs of pig disturbance were recorded in four 10 by 10 m quadrats over a standardized two-minute search period for each quadrat. For linear arrays on steep slopes, quadrats were positioned along a line transect, while in rectangular arrays quadrats were in a square configuration. In each quadrat the presence or absence of old and new signs of tracks, scat, digging and vegetation damage were recorded. New sign was defined as having likely occurred no later than two weeks prior, based on leaf fall on top of sign, desiccation of soil, layered disturbances, or other visual cues of time since the sign was produced. Disturbance surveys were conducted both upon the deployment and recovery of cameras from each site. Disturbance survey data was collated into a .csv file and the frequency of each type of sign recorded (tracks, scat, dig, etc.) was averaged for each site location to calculate the average of each type of recorded sign per site. The sum of the averages of each type of recorded sign per site (all sign) was then used as the second form of abundance data for model building.

Predictor variables:

Environmental and human-related predictor variables were chosen based on the expected ecological requirements of feral pigs and the influence of human interactions on feral pigs. In total, eight variables were chosen as predictors used in the modeling process: vegetation density,

vegetation height, mean annual rainfall, elevation, native vegetative cover, distance to ungulate fences, distance to hiking trails, and distance to forest. I used data obtained from the State of Hawaiʻi's Office of Planning, United States Geological Survey (USGS) Gap Analysis Project (GAP), the Rainfall Atlas of Hawaiʻi, and other layers provided by the Department of Land and Natural Resource's (DLNR) Division of Forestry and Wildlife (DOFAW) (Gergely and McKerrow, 2013; Giambelluca et al., 2012). Distance and density-related variables were manually generated from existing base features: USGS GAP Land Cover (30 m x 30 m), ungulate fence lines (DOFAW), and Na Ala Hele trail system (DLNR). These base features were used to generate the following variables as predictors: distance to forest (mesic and wet), native vegetative cover, distance to ungulate fence, and distance to trails. To generate distance-related variables, base features were rasterized from their original resolution to 500 m^2 and resampled using the method "majority" (Morelle and Lejeune, 2015). Distance-related variables were then created from these 500 m^2 raster layers using the Euclidean distance tool in ArcGIS. The distance to forest predictor layer was generated using only mesic and wet forests as the base USGS GAP Land Cover layer was unreliable in distinguishing between dry forests and sparse dry shrubland. Density-related variables ("native cover") were created by masking USGS GAP Land Cover data to any vegetative cover classified as "native" and resampling the base feature (30 m^2) to 500 m^2 using the method "bilinear" to calculate a density-related output (Hijmans et al., 2017). The vegetation height layer obtained from USGS GAP inadequately classified buildings in urban areas as tall vegetation which required reclassifying values associated with urban areas to 0 using the raster package in R (Hijmans et al., 2017). All predictor layers used in the analysis were standardized at 500 m^2 resolution as this was determined to be a good estimate of the mean home range size for feral pigs in Hawaiʻi and would allow each survey site to be

spatially independent. Collinearity between predictors was considered using pairwise Pearson coefficients (R^2) and any predictors with R^2 greater than 0.75 were excluded (Dormann et al., 2013; Elith et al., 2010).

Model development and validation:

Distribution models for both seasons were developed using the two most common forms of abundance data for pigs: (i) mean counts of camera-captured observations and (ii) sum of recorded sign. These two data sources were used as the response variable for a stepwise model fitting process. During this process, data were fitted to several types of regressive models with varying distributions to address model overfitting and issues associated with over or under dispersion (Hoef and Boveng, 2007). Dispersion can be defined as more variance than might be expected based on mean-variance scaling and is often present in abundnace data due to inherent heterogeneity of biological data (White and Bennetts, 1996). It is imperative to test for this additional variance as it can bias the mean values and standard errors of parameter estimates (Hilbe, 2011). To account for dispersion, different types of models can be fitted, in this case a generalized linear model (GLM) or a zero-inflated model. Additionally, these models can be fitted to different distribution types (Poisson or negative binomial) or additional predictor variables can be included to explain the unexpected variance. Abundance data were fitted to Poisson and negative binomial distributed GLMs from the 'stats' and 'MASS' (Venables and Ripley, 2002) packages in R (Poisson or NB) and zero-inflated mixture models (ZIP or ZINB) from the 'pscl' package (Zeileis et al., 2008) to account for issues with over or under dispersed data (Hijmans et al., 2017; R Core Team, 2019). Poisson and negative binomial distributions were chosen as biological count data most often best fit these distributions (Dénes et al., 2015; Lyashevska et al., 2016; Oppel et al., 2012; Wenger and Freeman, 2008; White and Bennetts,

1996). Zero-inflated models were included in the model fitting process as they provide a means of partitioning the model into two parts (zero component and count component) which help explain dispersion caused by false-negative counts (Dénes et al., 2015).

Predictor variable sets were constructed based on a priori hypothesis of response-predictor relationship and were fitted to models with increasing complexity (GLM to zero-inflated) until dispersion was appropriately accounted for and model overfitting was not present. Model predictions and outputs were visually assessed for any indication of predictor overfitting (Elith et al., 2010). Examples of overfitting include predictor distribution outputs mirroring the distribution and frequency of predictor variables. Predictor sets were constructed to consider first and second order relationships of predictor variables and interactions between predictors. The same predictor variable sets were used to identify best fit models for both spring and fall. Best-fit models were chosen based on Akaike Information Criteria (AIC) and the ratio of the sum of the squared Pearson's residuals henceforth referred to as the dispersion parameter (Anderson et al., 1994; Cox, 2018; Zuur et al., 2009). The dispersion parameter (φ) is calculated using equation 1 where φ values equal to one indicate no dispersion and values greater or less than one indicate over and under dispersion respectively (Zuur et al., 2009, pg. 226). Models with a dispersion parameter exceeding 1.5 were considered over dispersed and those with much <1.0 were considered under dispersed. These models were either corrected for dispersion by fitting different distributions (Poisson or negative binomial) or model types (GLM or zero-inflated) or else excluded from the model selection process. In total, over 20 predictor variable sets were constructed that underwent the model fitting process to identify best-fit models for both spring and fall datasets.

$$\varphi = \frac{\sum_i^n \varepsilon_i^2}{n-p} \tag{1}$$

Seasonal distribution

Only models using mean counts from camera-captured observations were used to quantify the effect of season on feral pig distribution due to the longevity of observable sign spanning greater than the season period. To identify the effect of season on the distribution of feral pigs on Maui the coefficients and significance of predictor variables were compared. Quantifying the significance and effect of predictor variables help identify which predictor variables are primary drivers of feral pig distribution between each season and their relationship (positive vs. negative). Best-fit models were then used in a predictive model framework to estimate expected feral pig abundances across the island of Maui for each 500 m^2 raster cell to produce seasonal distribution maps. These maps were then qualitatively and quantitatively compared. To quantitatively test for seasonal changes in habitat selection, distribution maps were standardized using the maximum abundance estimates between the two seasons to calculate a relative abundance index on a scale from 0 to 1. These standardized distribution maps were then subset into nine different habitat types as defined by the USGS GAP Land Cover dataset. Analysis of variance tests (ANOVA) were performed comparing spring and fall relative abundances within each of the habitat types to test for changes in habitat selection. P-values from ANOVA tests were adjusted using the Bonferroni correction factor to account for the number of habitat types tested (Bland and Altman, 1995).

Results

Seasonal conditions:

Spring (March 8th to June 5th, 2018) long-term mean monthly temperatures range from a low of 5°C in March to a low of 7.4°C in May. Mean monthly high temperatures range from 22.3°C in March to 24°C in May. March is typically the wettest month of the year with rainfall steadily decreasing through May. The upper limits of monthly rainfall peak at 1323 mm in the East Maui mountain range and 970 mm in the West Maui mountains in March and decrease to around a maximum of 700 mm in both mountain ranges by May. Making May typically one of the driest months of the year. During spring, the recorded temperatures at Maui weather stations compared to the 30-year averages reveal that the spring temperatures did not differ far from the normal (Fig 3.3). However, temperatures recorded at the higher elevation weather station in Kula did indicated slightly warmer temperatures than the expected. Average recorded rainfall over this period compared with long-term averages indicate that spring was far wetter than normal (Fig 3.3). It is important to note that this variation in rainfall is largely due to one storm event that occurred early-April 2018 which accounted for nearly half of all recorded rainfall for the three-month period. Excluding the April storm event, recorded rainfall was similar to expected long-term averages.

Fall (October 8, 2018 to January 4, 2019) long-term mean monthly temperatures ranged from a low of 5.9°C in December to 8.1°C in October. Mean monthly high temperatures ranged from 22.5°C in December to 25.3°C in October. Average rainfall over this three-month period is typically wetter than spring and maximum monthly rainfall remains around 1000 mm between both the East and West Maui mountains. Based on the expected conditions from long-term averages, fall is generally wetter and warmer than spring. However, cross-referencing expected long-term averages with those recorded at weather stations during this three-month period revealed that fall was slightly warmer than expected (Fig. 3.3). Similar to spring, the Kula

RAWS weather station exhibited the largest deviation of any weather station possibly indicating high elevations over both seasons were warmer than average. Furthermore, rainfall throughout fall was lower at all weather stations indicating a drier fall than expected.
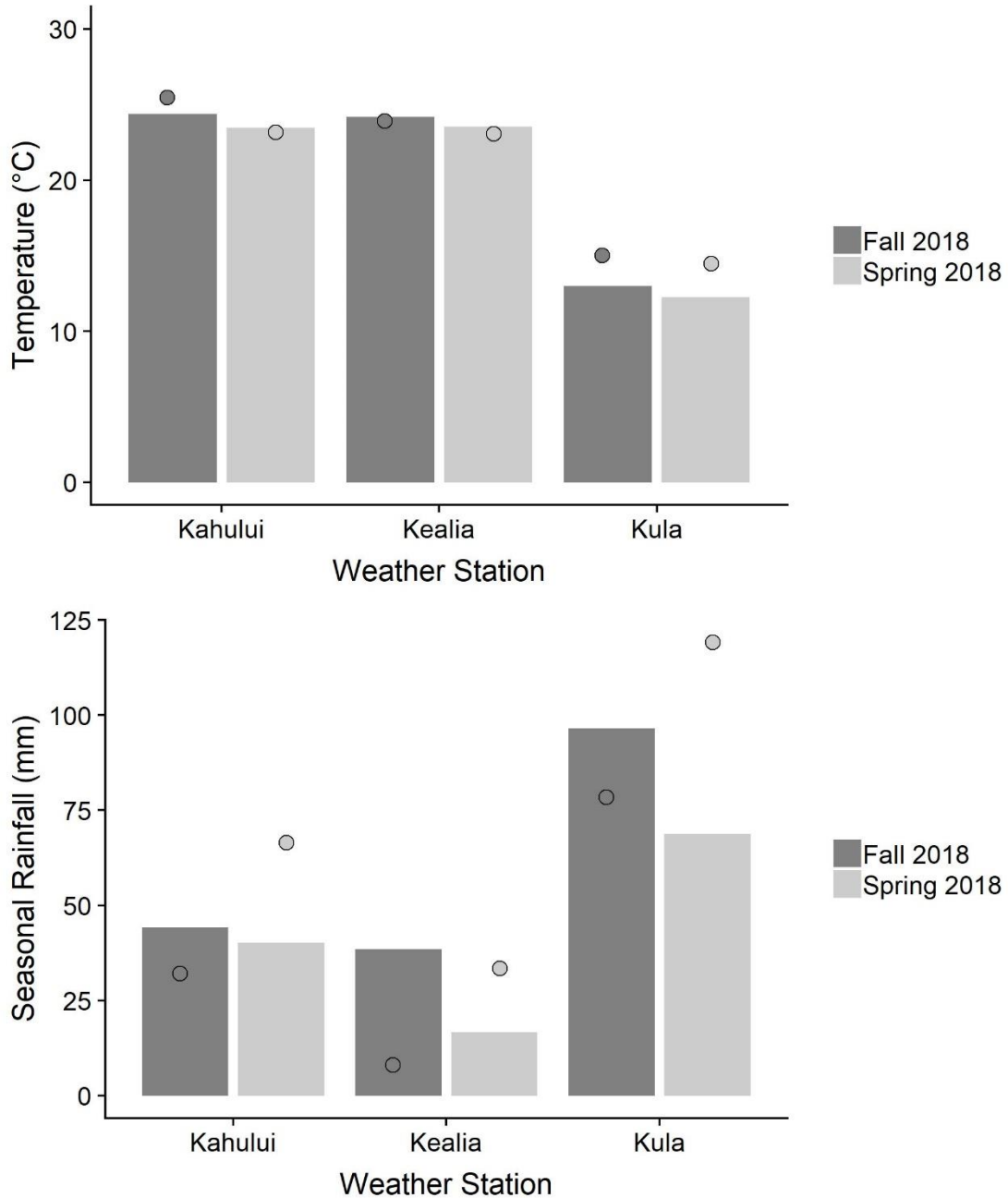
Fig. 3.3. Long-term averages (30yr) across three weather stations for each season of data collection. Long-term average data are denoted by bar plots shaded by season and observed

weather data collected from each weather station during the study period are displayed by points of identical color.

Basic stats

In total, 30 sites were visited during spring 2018 and 31 sites were visited during fall 2018. A total of 1,145,644 photos were taken by cameras traps for spring and 924,114 photos for fall. For spring, pigs were detected by camera traps at 18 sites with a mean of 62 ± 21 detections per site and a maximum of 1,882 detections at a single site. In comparison, pigs were detected by cameras at 24 sites for fall with a mean of 34 ± 9 detections per site and a maximum of 859 at a single site.

At 17 of the 18 sites where pigs were detected by camera traps for spring, pig sign was also recorded. Additionally, four sites had records of pig sign, but no pigs were detected by camera traps. All but one of the sites had records of pig sign for fall, however, an average of 15 ± 3 and 13 ± 2 signs of pig were recorded at sites where pig sign was present for spring and fall respectively. Both seasons had a maximum value of 38 recorded signs of pig presence at a single site.

Spring 2018 Model:

Four of the best-fit model configurations are represented in Table 3.1. Results from model-fitting indicate that spring camera data was negative binomially distributed due to AIC values being lower for all negative binomial distribution models when compared to Poisson distributed models (Table 3.2). Zero-inflated models generally performed better than generalized linear models using both camera detections and recorded sign as the response variable (Table 3.2).

The zero-inflated negative binomial distributed (ZINB) model with predictor set C was chosen as the best-fit model for spring camera data. This model did not have the lowest AIC value however all models with lower AIC values had low dispersion parameter values indicating under dispersion except for predictor set B with ZINB. The ZINB model using predictor set B was not chosen due to model estimates being abnormally high indicating signs of model overfitting. These models were not considered as best-fit models and predictor set C with ZINB was chosen due to its acceptable φ and next lowest AIC value. Predictor set B with ZINB was chosen as the best-fit model for spring recorded sign data due to near synonymous AIC values with the negative binomial distributed GLM (NB) with set D however, set B with ZINB had a more acceptable φ value. The NB model with predictor set D also showed signs of predictor overfitting due to high predicted values that were not representative of observed sign data.

Based on the final best-fit model for camera observation count data (Set C ZINB) the distribution of feral pigs on Maui for spring was most strongly driven by the amount of rainfall and vegetation height. These predictors were found to be the most significant variables out of the eight predictors used in the model fitting process. Rainfall had a significant negative model coefficient, indicating a decrease in the relative abundance of feral pigs with increasing amounts of rainfall (Fig. 3.4). Vegetation height had a significant positive model coefficient, indicating an increase in the relative abundance of feral pigs with increasing vegetation height. Vegetation height was also found to be a significant predictor for the zero component of the zero-inflated model. Vegetation height had a significant negative coefficient for the zero component indicating that with increasing vegetation height the probability of false zeroes decreases (Fig 3.4).

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Table 3.1. A sub-sample of the larger predictor variable set including the best-fit predictor sets for spring and fall recorded sign and camera-captured observations

	Predictors	
Predictor Set	Count component	Zero component
A	native cover*vegetation density	NA
B	vegetation height, elevation	vegetation height
C	annual rainfall, vegetation height	vegetation height
D	vegetation density, distance to forest	vegetation height

Note: The zero component terms for predictor sets that had them were excluded from GLMs and instead only the count component terms were used due to the inability to separately model the count and zero processes using GLMs.

Table 3.2. Results of best-fit models for camera observations and recorded sign data. A breakdown of predictor set configurations can be found in Table 2.1

Data	Distribution	Predictor Set	AIC	Δ AIC	φ
CAM	ZINB	B	196	0	1
CAM	NB	D	196	0	0.77
CAM	NB	B	198	2	0.89
CAM	ZINB	D	199	3	0.83
CAM*	ZINB*	C*	203*	7*	1.08*
CAM	NB	A	214	18	0.98
CAM	ZINB	A	216	20	1.02
CAM	NB	C	218	22	0.74
CAM	ZIP	B	659	463	8.3
CAM	ZIP	C	830	634	14.9
CAM	Poisson	B	866	670	28
CAM	ZIP	A	1197	1001	6.7
CAM	Poisson	C	1353	1157	62
CAM	ZIP	D	1552	1356	51.5
CAM	Poisson	D	1676	1480	75
CAM	Poisson	A	1751	1555	71.3
SIGN	NB	D	173	0	0.9
SIGN*	ZINB*	B*	174*	1*	1.03*
SIGN	ZINB	D	175	2	1.07
SIGN	ZINB	C	187	14	1.15
SIGN	NB	B	187	14	0.84
SIGN	ZINB	A	192	19	1.1
SIGN	NB	A	195	22	1.3
SIGN	ZIP	B	196	23	1.7
SIGN	NB	C	202	29	0.94
SIGN	ZIP	D	236	63	3.3
SIGN	ZIP	C	256	83	2.7
SIGN	Poisson	D	256	83	5.7
SIGN	ZIP	A	262	89	2.1
SIGN	Poisson	B	283	110	6.03
SIGN	Poisson	A	353	180	9.1
SIGN	Poisson	C	396	223	13.4

Note: ZINB = zero-inflated negative binomial distribution, ZIP = zero-inflated Poisson distribution, NB = generalized linear model (GLM) negative binomial distribution, Poisson = generalized linear model (GLM) Poisson distribution. * indicate best-fit models chosen for each dataset

Fig. 3.4. Response curves of predictor variables used in the best-fit model using mean counts of camera-captured observations for spring distribution of feral pigs on Maui. The top plots represent the count component of the zero-inflated model and predictor significance and correlation to predicted counts. The bottom-most plot is a representation of the zero component of the zero-inflated model representing the probability of false zeroes with increasing vegetation height. Estimates, standard errors (SE), and the p-values for each predictor variables used in the best-fit model are displayed in the legend.

Fall 2018 Model:

Generally, fall models fitted with negative binomial distribution performed better than those fitted to Poisson distribution. Zero-inflated models fitted with camera data as the response variable performed better than those fitted to GLMs. However, GLMs fitted with recorded sign as the response variable performed better than zero-inflated models. Most of the zero-inflated models using recorded sign as the response variable resulted in fitting errors for the count component of the zero-inflated model. This indicated that sign data observed during fall was not zero-inflated and the count component did not need to be partitioned from zero component.

Best-fit models for fall camera and recorded sign data were ZINB model with predictor set D and the NB model with predictor set A respectively (Table 3.3). AIC and φ values for ZINB and NB camera models using predictor set D were near synonymous. However, including an additional predictor (vegetation height) for the zero component of the ZINB model explained additional variation resulting in a more robust model output. Both NB models with predictor sets B and D were not chosen as the best-fit model for fall recorded sign data although they had lower AIC values than the NB model with set A. These models showed signs of predictor overfitting due to near synonymous distribution outputs as the predictors and artificially low p-values. The NB model with predictor set A was therefore chosen due to its acceptable AIC and φ values and realistic model outputs.

Based on the best-fit model for camera data for fall (ZINB set D) the distribution of feral pigs for fall was most strongly driven by vegetation density and the distance to forest (Fig. 3.5). Both vegetation density and distance to forest had a significant negative model coefficient indicating a decrease in the relative abundance of feral pigs with increasing vegetation density and the distance to forest (Fig 3.5). Vegetation height had an insignificant negative model

coefficient for the zero component of the zero-inflated model but was still included in the best-fit model as AIC and dispersion indicated a worse-fit model without it.

Table 3.3. Results of best-fit models for fall camera observations and recorded sign. A breakdown of predictor set configurations can be found in Table 2.1

Data	Distribution	Predictor Set	AIC	Δ AIC	φ
CAM	NB	D	240	0	1.24
CAM*	ZINB*	D*	241*	1*	1.24*
CAM	NB	B	244	4	1.24
CAM	NB	C	246	6	0.71
CAM	ZINB	A	247	7	0.9
CAM	ZINB	B	248	8	0.93
CAM	ZINB	C	249	9	0.83
CAM	ZIP	D	989	749	7.8
CAM	ZIP	B	1027	787	8.02
CAM	ZIP	A	1034	794	6.76
CAM	ZIP	C	1050	810	7.18
CAM	Poisson	D	1131	891	49.4
CAM	Poisson	B	1230	990	50.7
CAM	Poisson	A	1371	1131	54.1
CAM	Poisson	C	1486	1246	52.8
CAM	NB	A	NA	NA	NA
SIGN	NB	D	206	0	1.2
SIGN	NB	B	221	15	1.04
SIGN*	NB*	A*	222*	16*	1.03*
SIGN	ZINB	A	224	18	1.07
SIGN	NB	C	227	21	0.88
SIGN	Poisson	D	240	34	3.92
SIGN	Poisson	B	311	105	6.32
SIGN	ZIP	A	325	119	5.14
SIGN	Poisson	A	327	121	6.9
SIGN	Poisson	C	362	156	7.9
SIGN	ZINB	B	NA	NA	NA
SIGN	ZINB	C	NA	NA	NA
SIGN	ZINB	D	NA	NA	NA
SIGN	ZIP	B	NA	NA	NA
SIGN	ZIP	C	NA	NA	NA
SIGN	ZIP	D	NA	NA	NA

Note: ZINB = zero-inflated negative binomial distribution, ZIP = zero-inflated Poisson distribution, NB = generalized linear model (GLM) negative binomial distribution, Poisson = generalized linear model (GLM) Poisson distribution. * indicate best-fit models chosen for each dataset
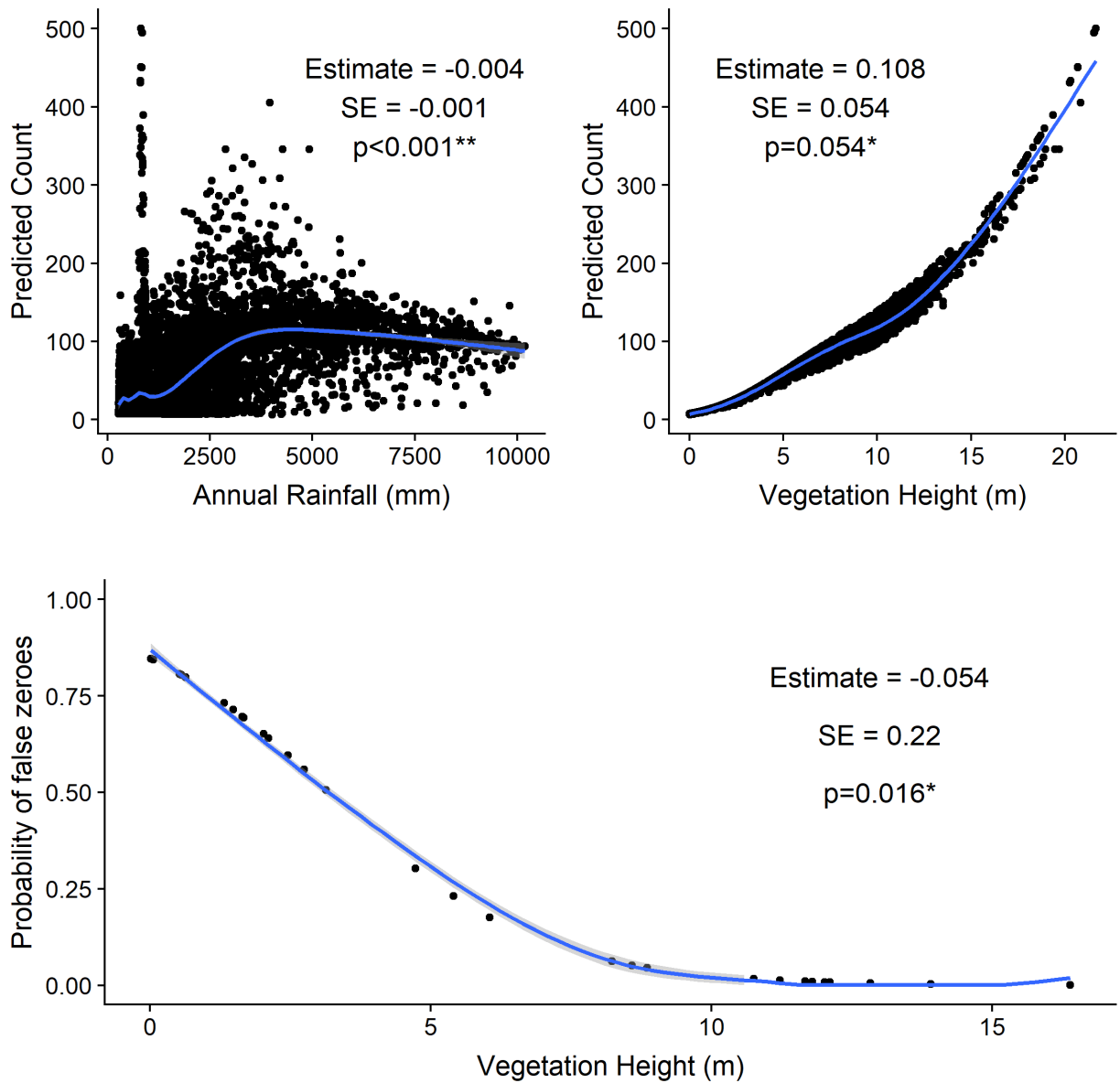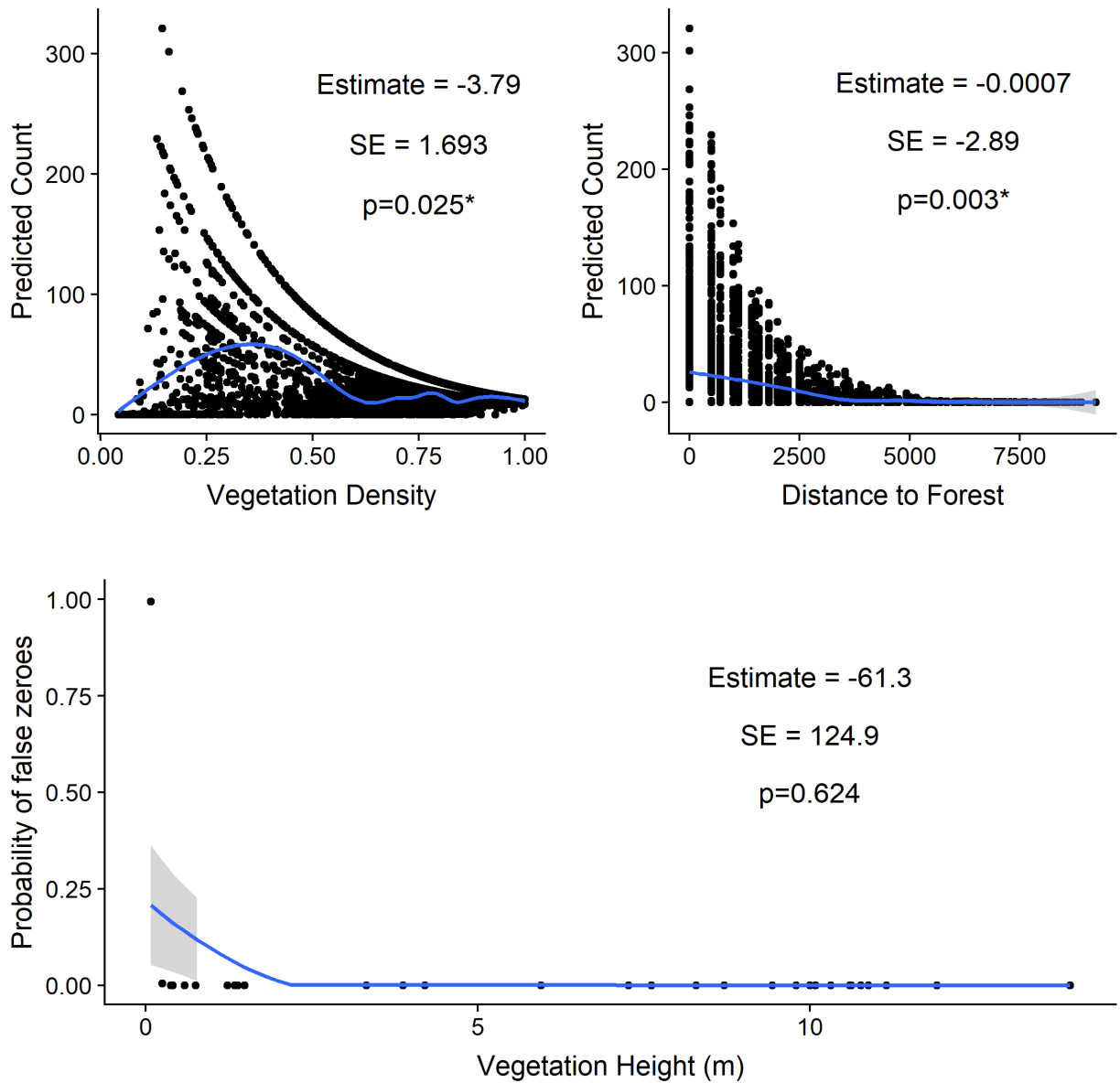
Fig. 3.5. Response curves of predictor variables used in the best-fit model using mean counts of camera-captured observations for fall distribution of feral pigs on Maui. Top-most plots represent the count component of the zero-inflated model and predictor variable significance and correlation with predicted counts. The bottom-most plot is a representation of the zero component of the zero-inflated model representing an insignificant relationship between the probability of false zeroes and increasing vegetation height. Estimates, standard errors (SE), and the p-values for each predictor variables used in the best-fit model are displayed in the legend.

Seasonal distribution

Fig 3.6, 3.7, and 3.8 present the distribution of feral pigs and their seasonal variation as predicted by ZINB and GLM models. Distribution maps for recorded sign, camera detections, and a standardized additive combined model are included, but quantitative spatial analyses were only performed on distribution maps generated from camera observations (Fig 3.7). Due to variability in the longevity of observable sign, distribution maps generated from recorded sign (Fig. 3.6) and combined additive models (Fig. 3.8) were excluded from the quantitative spatial analysis. Spring distribution maps show feral pigs to be most abundant in both the mixed alien forests of Kula and highly abundant throughout the northern and eastern slopes of Haleakalā (Fig. 3.6, 3.7, & 3.8). Pigs were mostly absent from the drier high elevations of Haleakalā and extensive areas of fallow agriculture of East and West Maui. Spring maps show pigs to be most abundant in dense mid-elevation wet and mesic forests of East and West Maui. Considerable abundances of pigs also occur in the lower elevation dry forests on the western slopes of East Maui. Spring distribution of feral pigs seemed to be highly constrained to forested areas and an analysis of variance (ANOVA) indicate a significant shift outside of these land cover types during fall. Fall maps show a shift in pig distribution to higher elevations of Haleakalā dominated by dry and mesic shrubland (Fig. 3.9). Pig abundance seemed to be less constrained by forested cover and more constrained by the distance to forest as indicated during model development. ANOVA revealed significant shifts in pig abundance from native wet and mesic forests and alien forests into more open native mesic shrubland between spring and fall (Fig. 3.9). Overall distribution during fall for models generated from camera data appear to be more highly constrained to distinct habitat types than spring (Fig. 3.8).
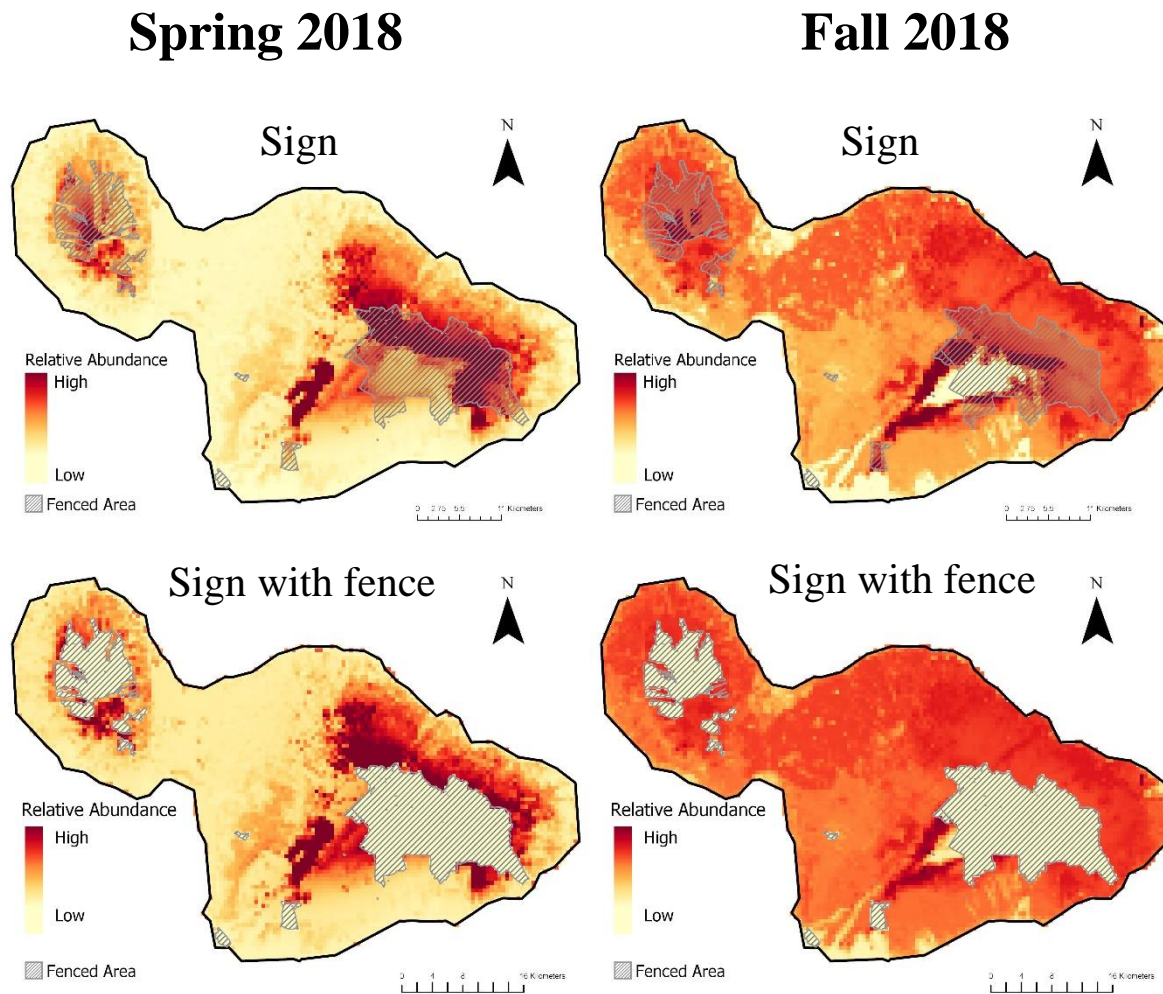
Fig. 3.6. Feral pig distribution maps generated from the best-fit models for spring (left) and fall (right) using recorded sign abundance data. Maps were created using all available land-area without excluding existing ungulate proof areas (top) and excluding ungulate proof areas (bottom).

Spring 2018

Fall 2018
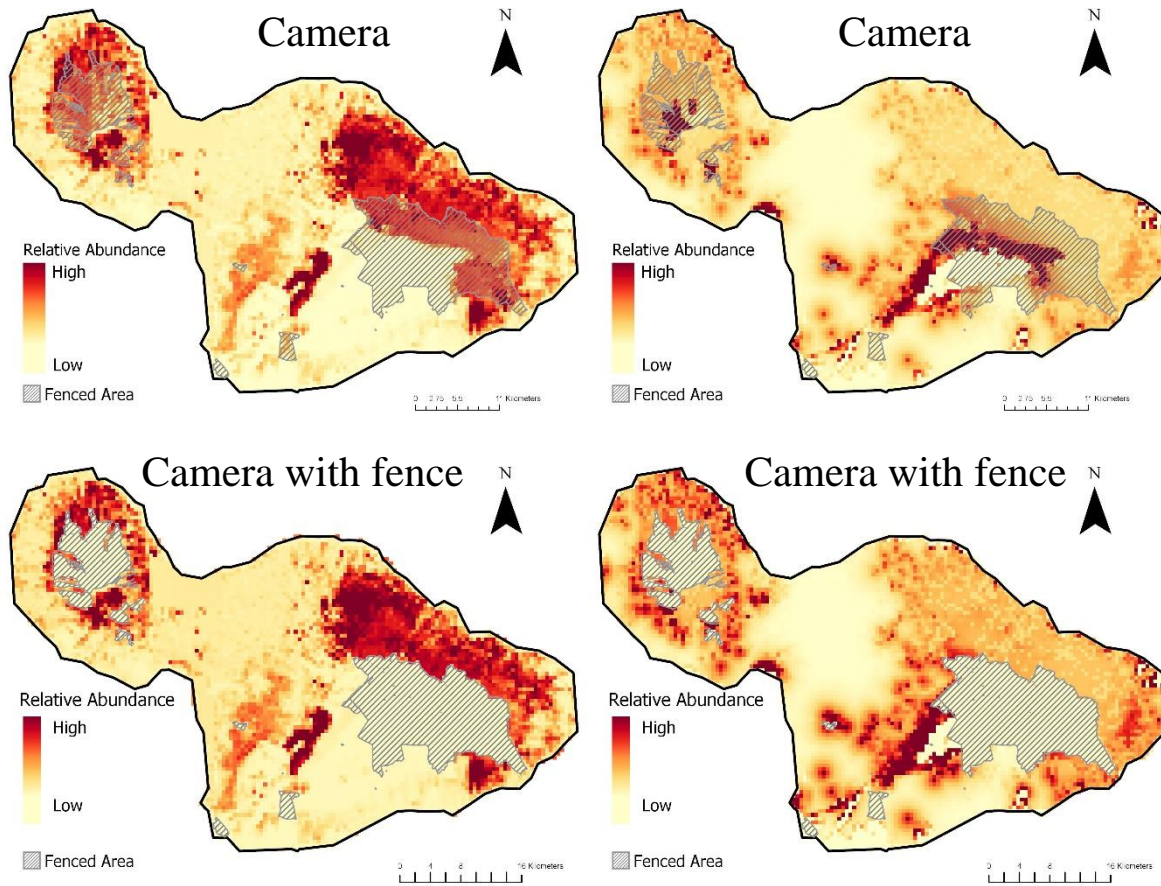
Fig. 3.7. Feral pig distribution maps generated from the best-fit models for spring (left) and fall (right) using abundance data recorded by game cameras. Maps were created using all available land-area without excluding existing ungulate proof areas (top) and excluding ungulate proof areas (bottom).
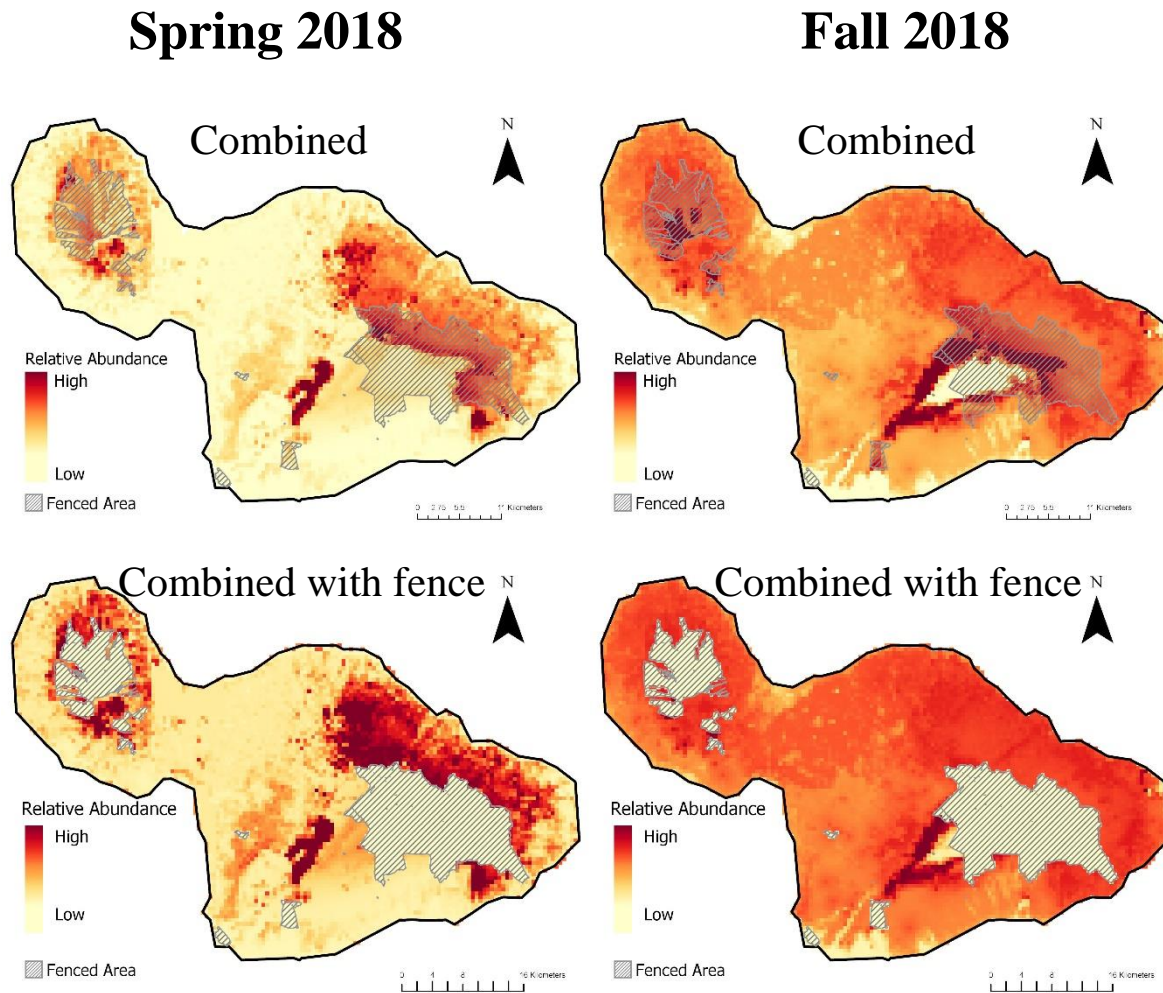
Fig. 3.8. Feral pig distribution maps generated from the best-fit models for spring (left) and fall (right) using a standardized additive combined model of both abundance data types. Maps were created using all available land-area without excluding existing ungulate proof areas (top) and excluding ungulate proof areas (bottom).

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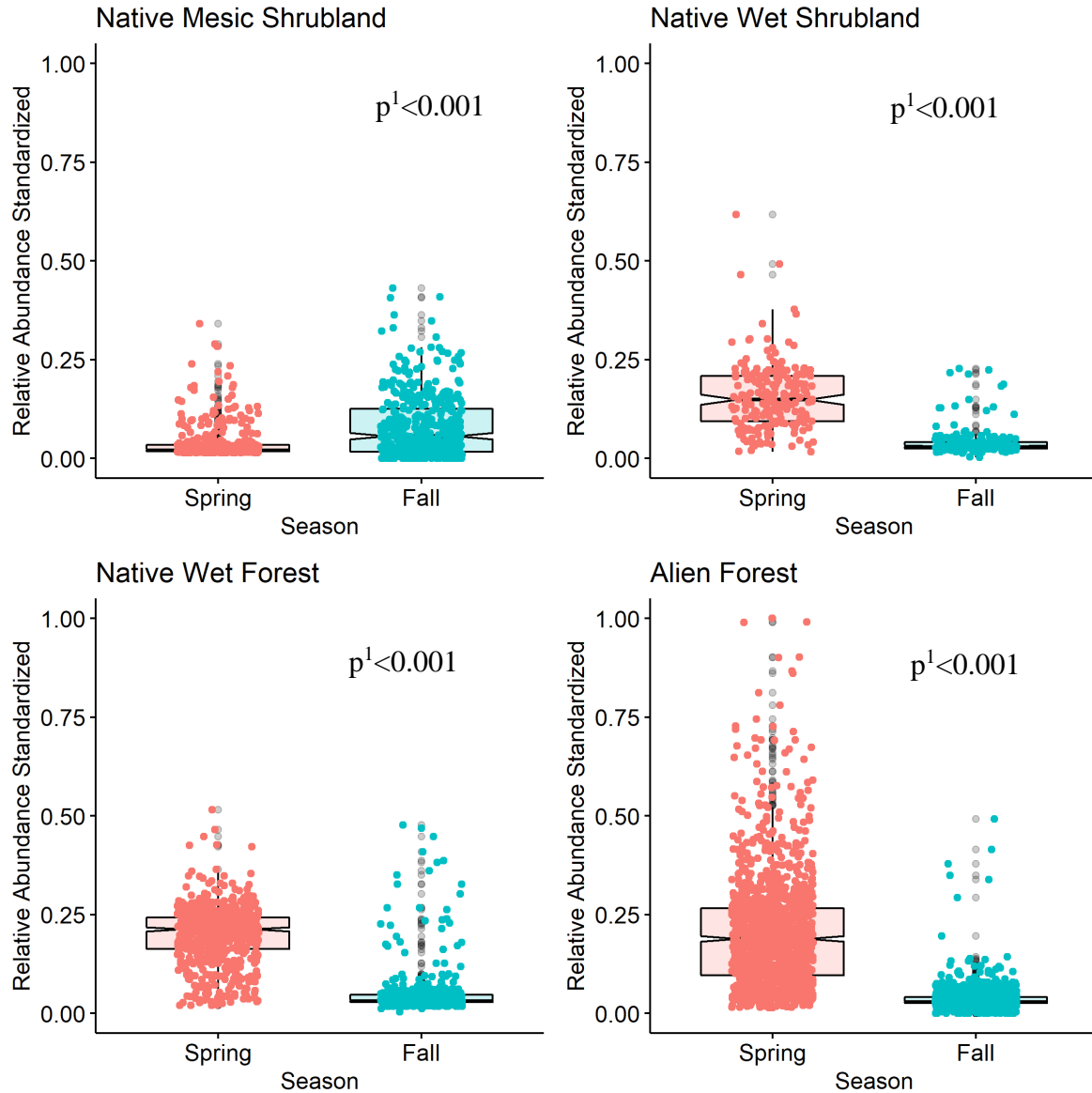
Fig 3.9. Predicted relative abundance of feral pigs using mean counts from camera-captured observation models during spring (pink) and fall (blue). Points show the distribution of the data and each box represents the upper and lower interquartile range (25% and 75%) of the data. Notches represent the median values for each season. [1]P values from ANOVA tests are reported in the top right of the boxplots. [1] indicate p-values adjusted for number of habitat types tested using Bonferroni correction factor.

Discussion

Distribution maps generated from both forms of count data (mean camera captured observations and recorded sign) yielded significant relationships to environmental predictors. Model validation indicated each model performed well in predicting the overall distribution of feral pig relative abundance across the island of Maui. ZINB models and ANOVA on predicted counts generated from camera data showed a significant difference in the distribution of feral pigs and a significant shift in habitat selection between spring (March to May 2018) and fall (October to December 2018) supporting my first hypothesis that feral pig distribution would significantly differ between seasons.

The spring models indicate the importance of the amount of rainfall, elevation, and the height of vegetation as predictors for the abundance of feral pigs. Both maps generated from camera detections and recorded sign data were comparable in their distribution of pig abundance and support my hypothesis regarding the importance of cover for spring. Model results suggest that pigs are largely abundant throughout densely vegetated forests with tall vegetation (high canopy). Interestingly, the highest detections observed during this study period, in the forests of Kula, were seven times greater than the maximum detections in previous studies on Oʻahu where these types of forested areas do not occur (Risch et al., in review). These results are consistent with continental studies that determined similar forested habitats were commonly selected by feral pigs (Bratton, 1975; Fonseca, 2007; Rodrigues et al., 2016). Previous studies suggested these areas may offer protection from human disturbance, provide thermal cover in colder climates, and contain abundant sources of food (Merli and Meriggi, 2006; Thurfjell et al., 2009). The mixed alien forests found in Kula are rare in the Hawaiian Islands but may play a role in

supporting high densities of feral pigs through the provision of cover from hunters, warmer temperatures during cooler seasons, and substantial foraging opportunities.

Recreational activities and hunting pressure have been shown to have a significant impact on ungulate behavior, selectively shifting their home ranges to areas with increasing cover to avoid detection (Merli et al., 2017; Mysterud and Østbye, 1999; Stankowich, 2008). spring coincided with the game mammal hunting season for all hunting reserves. Interestingly, feral pigs were most abundant in forested areas just outside of the boundaries of many of the hunting units, suggesting a shift in movement from hunting pressure. These findings are consistent with studies in Europe that found feral pigs preferentially selected non-hunted areas during hunting periods (Rodrigues et al., 2016). More broadly, hunting during this season may have influenced the distribution of pigs, as they were generally most abundant in forested areas that provide protection and cover.

Temperature has also been found to be a key limiting factor in the distribution of pigs in the contiguous U.S. (McClure et al., 2015) and throughout Europe (Fernanda Cuevas et al., 2013; Fernández-Llario, 2004). Pigs commonly seek refuge in areas with continuous cover to thermoregulate when the air temperature is too high or too low (van Beest et al., 2012). Although temperature was not chosen as a predictor due to its autocorrelation with elevation, elevation was found to be a significant predictor for the recorded sign model. Spring long-term climate averages and recorded weather station data indicate slightly cooler temperatures when compared to fall, which along with increased hunting pressure may have led to the concentrated abundances of feral pigs in the mid to high elevation mixed alien forests.

Foraging opportunities also play a crucial role in the distribution and foraging behavior of feral pigs (Fonseca, 2007; Morelle and Lejeune, 2015; Rodrigues et al., 2016). Forested areas are

typically abundant in food resources for feral pigs when compared to more open shrublands and agricultural lands (Mysterud and Østbye, 1999). Forested areas provide feral pigs with both aboveground and belowground sources of food. Ground cover in continental hardwood forests are typically comprised of herbaceous plants that provide feral pigs with grazing opportunities and also transfer energy reserves to belowground tubers, bulbs, and rhizomes consumed by pigs through rooting and digging (Howe and Bratton, 1976; Small and McCarthy, 2003). The soil of most hardwood forests host a diverse assemblage of insects and earthworms as well as smaller rodents frequently seen in the stomach contents of feral pigs (Baubet et al., 2003; Cheong H. Diong, 1982; Jokimäki et al., 1998; McShea et al., 2003). Anecdotally, ground cover was largely absent from the alien hardwood forests on Maui potentially indicating a heavier reliance on rooting and digging for belowground biomass (e.g. earthworms) than grazing for aboveground biomass. Although not explicitly quantified in this study, the foraging opportunities present in these heavily forested areas, most notably the mixed alien forests in Kula, may have had important implications in the foraging behavior and distribution of feral pigs between both seasons.

Based on predictor significance, fall models stress the importance of vegetation density, native cover, and the distance to forest (mesic and wet) in predicting the abundance of feral pigs. Model results show a negative effect of vegetation density and the distance to forest on the abundance of feral pigs potentially indicating a shift in home ranges from spring. Additionally, vegetation height was not found to be a significant predictor indicating less reliance on the protection and resources these forested areas offer and potentially a shift in foraging behavior. Both results support my initial hypothesis that pigs would be less reliant on areas that provided vegetative cover. However, I did not anticipate fall distributions to be so constrained to a single

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habitat type. ANOVAs on the abundance of pigs by habitat type revealed a significant decrease in feral pig abundance in native wet and mesic forests and a significant increase in the abundance of pigs in open native mesic shrublands, particularly at higher elevations of East Maui.

Fall 2018 coincided with the closure of game mammal hunting in some of the most frequented hunting units like Polipoli springs State Recreational Area in the Kula Forest Reserve. The closure of hunting during this time may explain the shift in pig distribution outside of the forested safe havens and out into more open terrain as a result of effectively zero hunting pressure. Air temperatures for fall were also warmer on average than those in spring which could also be a contributing factor to the change in habitat selection. Finally, drier than average conditions for fall could have played a crucial role in feral pig foraging behavior. Abáigar (1993) found that in drier conditions feral pigs will actively shift their foraging behavior to primarily grazing as belowground resources are difficult to extract from dry soil. This might help explain the significant increase in feral pig abundance in open mesic shrublands during fall which provide more grazing opportunities than the denuded and often absent ground cover of mixed alien forests.

Although not used in the seasonal comparison analysis, distribution maps generated from the recorded sign model show a much broader distribution of feral pigs when compared to the model generated from camera detections (Fig. 3.6 & 3.7). This could be largely due to environmental conditions that influence the detectability of sign and the longevity of its presence. Fall conditions were drier than normal based on long-term climate averages, which may have increased detectability of older signs of feral pig presence, as a result of reduced exposure to weathering. Consequentially, sign was more frequently recorded across all fall sites when compared to spring. This finding further supports the exclusion of recorded sign models

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from the seasonal analysis, as older feral pig signs may have been produced outside of the sampling period and therefore would not be representative of their distribution during that season.

Although I did not anticipate feral pig distribution to be so highly constrained to open mesic shrublands during fall, my results show a significant shift in feral pig distribution between seasons on Maui and hint at a potential shift in foraging behavior. There are at least two potential explanations for the differences between spring and fall distributions: (1) hunting pressure may influence ungulate behavior; (2) changes in environmental conditions may influence feral pig foraging behavior by shifting food availabiltity. The significant differences in feral pig abundance, particularly around the game mammal hunting units that were closed between each season lends substantial support to the first explanation. However, abnormally low rainfall and greater than average temperatures during fall may have shifted food resources, providing support to the second explanation. I expect that each of these changes in conditions worked in concert and influenced the distribution of pigs across the landscape. Finally, regardless of changes in feral pig distribution it is apparent that mixed alien forests support significantly higher abundances of feral pigs in relation to all other habitat types. Special attention should be placed on these areas as this study shows high abundances of feral pigs in these alien forests which move into adjacent sensitive native shrublands throughout the year. These native habitats host a variety of endangered endemic species and are of the utmost importance for achieving conservation goals.

Management Implications

The results from this thesis chapter offer insight into how seasonality can influence the spatiotemporal variation of a valued game mammal and problematic invasive species.

Management actions that incorporate this variation into the decision-making process will improve the likelihood of successful conservation actions (e.g. location of ungulate fences) and help inform seasonal management of game mammals (e.g. opening and closure of hunting seasons or increasing/decreasing bag limits throughout a calendar year). Results from this chapter allude to a relationship between the distribution and abundance of feral pigs and the presence of hunting pressure. Although causality is difficult to quantify, the closure of certain hunting units during the fall season appeared to have a considerable influence on the distribution of pigs within those units. For example, Fig. 3.7 show pigs to be more abundant in higher elevations of the Kula FR after the closure of the hunting units there. Future management might consider year-round hunting due to a significant shift in pig distribution from non-native habitat into sensitive native ecosystems that coincided with the closure of certain hunting units during the fall. More generally, this chapter shows that incorporating temporal variation into spatial models significantly influences model outputs and subsequent management recommendations based on those models. Researchers should continue to study how the inclusion of temporal variability influences outputs from spatial models and the implications they have for achieving conservation and game management goals.

CHAPTER 4

Conclusions

The geographic distribution of feral pig populations has expanded over recent decades, resulting in an increase in economic and ecological impacts. Further, the global distribution of suitable habitat for feral pigs is expected to increase due to climate change (Lewis et al., 2017). However, given the increased research attention wild pigs have received over recent years due to their expanding distribution, knowledge gaps remain in their basic biology, ecology, and the damages they cause to natural environments (Beasley et al., 2018). This information is essential in developing appropriate management strategies to prioritize where their damages are greatest and what methods can be implemented to best reduce their impacts. In my thesis, I have framed my research questions for chapter 2 and chapter 3 to address the most prevalent knowledge gaps for wild pig research as described by Beasley et al. (2018).

In chapter 2 of my thesis, I quantified the extent of wild pig impacts to all species assessed by the IUCN Red List. The Red List is the most comprehensive species assessment and has been extensively used in the area of invasive species impact analysis. However, the impacts of wild pigs have only partially been assessed, leading to a low ranking of wild pig threat among other problematic invasive species (Doherty et al., 2016). The comprehensive threat analysis contained in chapter 2 supports a growing body of research literature, suggesting wild pigs have ecosystem level impacts and threaten a wide variety of species through several threatening mechanisms. The results from this study also show the impacts from wild pigs to be comparable to invasive species that receive far more research attention and management. These results are important to address the knowledge gaps regarding wild pig impacts and the lapse in conservation efforts to mitigate them.

In chapter 3 of my thesis, I examined the spatiotemporal ecology of feral pigs across two seasons on the second largest main Hawaiian island. The results of this study provide important methods for monitoring feral pig populations and modeling their distribution. I found that the distribution and optimal habitat selected by feral pigs significantly differed between seasons. In addition to a quantitative analysis on feral pig abundances by habitat type, I was also able to produce predictive distribution maps depicting the difference in seasonal distribution of feral pigs. These results are important for resource managers who are tasked with mitigating the threats from feral pigs in high conservation value areas while also allowing feral pig populations on public lands for recreation and game management.

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