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Environmental drivers of seasonal shifts in abundance of wild pigs (*Sus scrofa*) in a tropical island environment

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Abstract

Background: Non-native wild pigs (*Sus scrofa*) threaten sensitive flora and fauna, cost billions of dollars in economic damage, and pose a significant human–wildlife conflict risk. Despite growing interest in wild pig research, basic life history information is often lacking throughout their introduced range and particularly in tropical environments. Similar to other large terrestrial mammals, pigs possess the ability to shift their range based on local climatic conditions or resource availability, further complicating management decisions. The objectives of this study were to (i) model the distribution and abundance of wild pigs across two seasons within a single calendar year; (ii) determine the most important environmental variables driving changes in pig distribution and abundance; and (iii) highlight key differences between seasonal models and their potential management implications. These study objectives were achieved using zero-inflated models constructed from abundance data obtained from extensive field surveys and remotely sensed environmental variables.

Results: Our models demonstrate a considerable change in distribution and abundance of wild pigs throughout a single calendar year. Rainfall and vegetation height were among the most influential variables for pig distribution during the spring, and distance to adjacent forest and vegetation density were among the most significant for the fall. Further, our seasonal models show that areas of high conservation value may be more vulnerable to threats from wild pigs at certain times throughout the year, which was not captured by more traditional modeling approaches using aggregated data.

Conclusions: Our results suggest that (i) wild pigs can considerably shift their range throughout the calendar year, even in tropical environments; (ii) pigs prefer dense forested areas in the presence of either hunting pressure or an abundance of frugivorous plants, but may shift to adjacent areas in the absence of either of these conditions; and (iii) seasonal models provide valuable biological information that would otherwise be missed by common modeling approaches that use aggregated data over many years. These findings highlight the importance of considering biologically relevant time scales that provide key information to better inform management strategies, particularly for species whose ranges include both temperate and tropical environments and thrive in both large continental and small island ecosystems.

Keywords: Ecology, Spatial, Temporal, Species distribution modeling, Wild boar, *Sus scrofa*, Feral pigs

Background

Native to Eurasia, wild pigs (*Sus scrofa*) have been identified as one of the most prolific large mammals on the planet due to their domestication around 9000 years ago (Larson et al. 2005) and subsequent human-facilitated introductions to novel ecosystems for food provisioning

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and livestock (Barrios-Garcia and Ballari 2012). As a result, wild pigs have established populations on six out of the seven continents and have been documented in a multitude of climates ranging from the tropics of Oceania and the Caribbean to the more temperate regions of Scandinavia and Canada (IUCN 2021). Recently, wild pig populations appear to be increasing throughout their native and introduced ranges and are beginning to recolonize areas throughout Europe that have been devoid of wild pigs for centuries (Saito et al. 2012; Massei et al. 2015). Similarly, over the past few decades regions throughout North America are experiencing increasing populations. Invasive wild pig populations have expanded northward from their introduction in the southern United States to states as far north as New Hampshire and Michigan and the Saskatchewan and Manitoba provinces of Canada (Brook and Beest 2014; Bevins et al. 2014; McClure et al. 2015; Snow et al. 2017).

The expansion of wild pig ranges and increasing populations have had an influence on the extent of both human–wildlife conflicts and the threats wild pigs pose to resident flora and fauna (Barrios-Garcia and Ballari 2012). Among the most problematic conflicts between humans and wild pigs are their ability to damage agricultural crops, collisions with vehicles, and capacity to transmit disease (Barrios-Garcia and Ballari 2012; Bevins et al. 2014; Keiter and Beasley 2017). Although data on the economic impacts and damage to agricultural crops are limited, the economic losses are substantial, varying from \$190 million a year in crop losses across 11 U.S. States (Anderson et al. 2016), \$61 million a year in damages in just the state of Georgia, U.S.A. (Mengak 2012), \$10,146 per landowner in the state of Texas, United States (Adams et al. 2005), and \$100 million per year in Australia (Choquenot et al. 1996). Based on limited data, Pimental (2007) estimated that wild pigs cost the United States \$1.5 billion annually as a result of damages caused by wild pigs and the costs to control these wild populations. Their ability to carry and transmit pathogens also poses a considerable and yet vastly understudied threat to humans, livestock, and resident flora and fauna (Bevins et al. 2014; Perroy et al. 2021).

Aside from human–wildlife conflicts, wild pigs are among one of the most damaging species to natural areas and the flora and fauna that reside there. Recently, wild pigs were identified as threatening 672 species globally and were implicated in the declines of 414 species of conservation concern, including 14 extinction events (Risch et al. 2021). Threats from wild pigs are indiscriminate, threatening a wide variety of species through direct predation, habitat disturbance, disease transmission, competition with other species, and hybridization with other species in the Suidae

family (Risch et al. 2021). These threats are persistent throughout their introduced and native ranges and anticipated to increase (McClure et al. 2018). A recent study by O'Bryan et al. (2021) also suggests wild pigs play a role in contributing to climate change through the release of CO₂ stored in soil. Thus, management of wild pigs is a global issue, impacting multiple sectors as diverse as agriculture, wildlife conservation, forestry, and private landowners.

In spite of this growing interest in increasing wild pig populations and their subsequent impacts, there remain large gaps in our understanding of their basic biological requirements and ecological interactions (Beasley et al. 2018). In particular, data on the spatial and temporal ecology of pigs across the diversity of habitats they occupy are sparse, and most efforts have taken place at large spatial scales that might not be useful for developing regional or site-specific management strategies for agencies on the ground (Beasley et al. 2018). For local management strategies to be effective, managers must have an adequate understanding of both the distribution and abundance of the target species (Yañez-Arenas et al. 2012; Ureña-Aranda et al. 2015). Understanding these two components of an invasive species allows for the subsequent prioritization of targeted control efforts (e.g., aerial shooting, exclusion fencing, Judas pig method) ultimately minimizing control costs and increasing the effectiveness of control efforts (Beasley et al. 2018). Furthermore, an understanding of the distribution and abundance of wild pig populations in relation to environmental conditions may shed light on the potential for pig populations to expand into favorable surrounding areas (McClure et al. 2015, 2018; Snow et al. 2017). Most studies have taken place within the continental United States, Europe, or Australia (Hone 2002; Mitchell et al. 2007; Morelle and Lejeune 2015; McClure et al. 2015; Lewis et al. 2017; Froese et al. 2017; Amendolia et al. 2019) and few studies have addressed these issues in island environments (Risch et al. 2020).

Species distribution models are an increasingly recognized tool to address spatial and temporal challenges in managing both species of conservation concern and invasive or pest species (Guisan et al. 2013; Tulloch et al. 2015). Distribution models allow individuals to quantify a correlation between the presence or abundance of a species and its surrounding environment. Using these correlations researchers are then able to predict likelihood of presence or relative abundance to areas outside of the sampled locations. These approaches have been widely used in the past several decades to great success in identifying previously undiscovered populations of threatened species (Raxworthy et al. 2003; Bourg et al. 2005), controlling problematic species (Aragón et al. 2010), and

quantifying the likelihood of invasion of non-native species (Barbet-Massin et al. 2018).

To date, the application of distribution models to help manage wild pig populations has been limited. There have been several large-scale modeling attempts that identified distribution and abundance of wild pigs at the country or global scale (McClure et al. 2015, 2018; Snow et al. 2017; Lewis et al. 2017) and these efforts have shed light on critical issues regarding current wild pig populations, their potential for expansion, and species at-risk. However, due to their large-scale (country, continent, or global), the coarse resolution of these outputs, they may not be useful to decision-making for smaller municipalities or regions.

Furthermore, these large-scale efforts often use an accumulation of data acquired from numerous surveying efforts over long time scales, compressed into models that do not account for temporal nuances. Using Maxent, a presence-only based modeling approach, Morelle and Lejeune (2015) and Amendolia et al. (2019) identified changes in seasonality of wild pig occupancy at relatively fine scales (regional or natural reserve) in Belgium and Italy, respectively. Their approach shows the potential for modeling changes in the distribution of wild pigs throughout time, to better inform management decisions. Similarly, Risch et al. (2020) used established methods of monitoring wild pigs to estimate a relative abundance metric and model the distribution of wild pigs across a large Hawaiian island. Metrics of relative abundance are important from a decision-making perspective as it allows managers to prioritize areas based on the expected abundance of animals, in contrast to Maxent type approaches (e.g., presence-only, presence-absence) that provide information on the likelihood of occupancy. However, to our knowledge, the temporal principles applied in the Morelle and Lejeune (2015) and Amendolia et al. (2019) studies have not yet been applied to an abundance modeling approach for wild pigs.

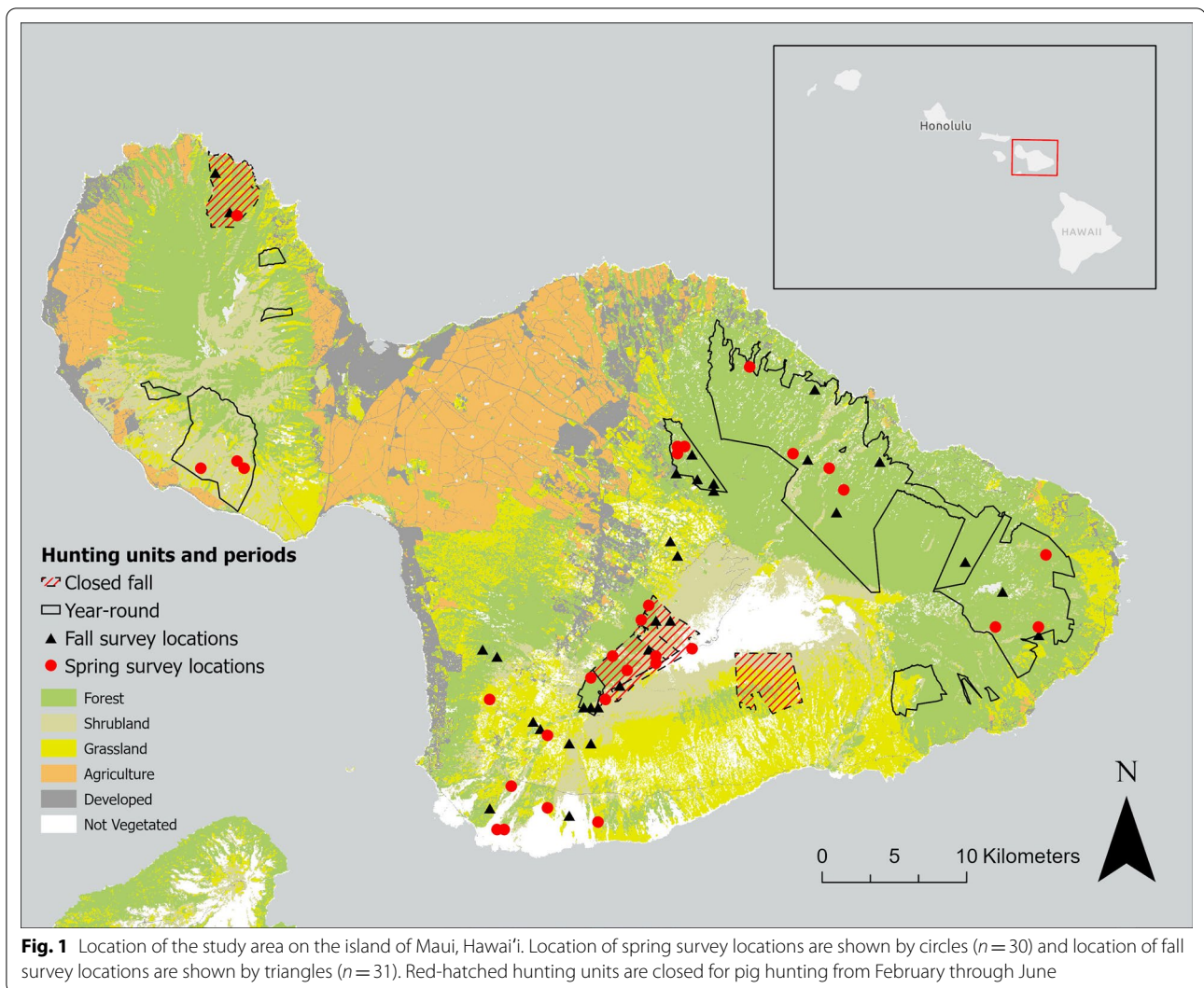
Here, we aimed to incorporate the principles applied in Morelle and Lejeune (2015) and Amendolia et al. (2019), principally the inclusion of biologically relevant time intervals, and apply them to the relative abundance modeling framework established by Risch et al. (2020). In this study, we used data of wild pigs captured by camera traps across two seasons (spring and fall) to quantify their relative abundance and subsequently model and compare seasonal distribution trends. We aimed to identify differences in the seasonal distribution of wild pigs and the underlying environmental conditions driving those changes, to elucidate the potential utility of modeling relative abundance of wild pigs at finer resolutions across relevant temporal gradients and their resulting applications to game and wildlife management. A better

understanding of the processes driving the distribution and abundance of wild pigs throughout space and time are essential to mitigate the impacts of wild pigs on sensitive flora and fauna and to minimize human-wildlife conflict.

Methods

Study area

The island of Maui is the second largest Hawaiian Island and has a land area of 1883 km² (Fig. 1). There are two main mountain ranges, the West Maui mountains with elevations up to 1764 m and East Maui mountains (Haleakalā) with elevations up to 3055 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. Coastal and low elevation areas are generally dominated by developed or agricultural lands. Large swaths of areas classified as agriculture are in fact fallow sugar cane fields as a result of the demise of the sugar cane industry in the late twentieth century and eventual closure in 2016. Mid-elevations generally comprise either mixed (native and non-native) forest or shrublands while much of the forested northern slopes of Haleakala remain relatively intact (native plant-dominated). Sub-alpine areas on Haleakalā are dominated by native shrublands and serve as some of the last remaining habitat for a number of threatened and endangered species (United States Fish and Wildlife Service 2016). There are three other wild ungulate species present on Maui, including Axis deer (*Axis axis*), feral goats (*Capra hircus*), and feral cattle (*Bos taurus*), all of which are non-native. Axis deer are widely abundant throughout mid to low elevation shrublands and agricultural lands while feral goats dominate arid sparsely vegetated areas from coastal to sub-alpine areas. The presence of feral cattle is typically site-specific, resulting from escaped or illegally released animals. There are no natural predators of wild ungulates, but wild dog populations have been known to cull some animals



and there is an active hunting community (Luat-Hū'eu et al. 2021; Luat-Hū'eu 2020).

Species abundance data

The relative abundance of wild pigs was calculated from data obtained from two seasons of intensive camera trapping effort in 2018 across the island of Maui, Hawai'i per the methods described by Risch et al. (2020). Survey locations for each season were separately selected using a stratified random sampling design. An equal number ($n = 15$) of survey locations were randomly selected across each of three altitudinal bands (0–999 m, 1000–1999 m, and 2000–3055 m) for each season resulting in 45 potential survey locations each for spring and fall of 2018. Survey locations were a minimum distance of 500 m from one another to ensure spatial independence. This minimum distance was chosen as it was determined

to be a reasonable estimate of pig home range size in Hawai'i (Salbosa and Lepczyk 2009), while also retaining a relatively fine spatial resolution. At each survey location, six game cameras (Bushnell Trophy Cams, Bushnell, Overland Park, KS) were distributed at 50-m intervals to maximize the detection probability of capturing wild pigs within the area. Six cameras were chosen as our previous efforts indicated this number of cameras was likely a conservative estimate to appropriately capture site-level variation of wild pigs (Ringma et al. 2017). Cameras were deployed at waist height on surrounding vegetation or on poles in the absence of vegetation. Cameras were deployed in a similar manner (angle, depth of view, height) across all survey locations to ensure detection probability remained constant. In cases where randomly selected survey locations could not be safely accessed, the site was moved to the closest analogous location within

500 m or else was excluded from the study. Camera traps were deployed in either the spring (March–May) or fall (October–December) of 2018 and a total of 30 and 31 locations (total=61 unique locations) were surveyed for each season, respectively. Camera trap data are commonly used to calculate a relative abundance index (RAI) for the target species, typically calculated as the number of observations per camera trap days (O'Brien et al. 2003; Palmer et al. 2018). As the number of camera trap days was standardized (2 weeks) across all survey locations for this study, we calculated the relative abundance of wild pigs at each site by averaging the total number of camera captured observations by the number of cameras deployed at each survey location. The resulting RAI, hereafter referred to as 'abundance data', was used as the response variable in the modeling process.

To address differences in the distribution and relative abundance of wild pigs throughout the survey period, we partitioned the dataset into three biologically relevant time intervals (spring, fall, combined). The spring (March–May) and fall (October–December) represent unique differences in the availability of food types (i.e., fruiting period), temperature, rainfall, and hunting pressure (open vs. closed). Many of the most common fruits (*Psidium cattleianum*, *Passiflora tarminiana*) in Hawai'i typically exhibit peak fruiting from December to April, coinciding with the data collected during the spring. These fruits are a common food source for wild pigs and are thought to play a role in driving range shifts throughout the year (Diong 1982; Wehr et al. 2018). Similarly, the months during the fall survey period are typically characterized by wetter conditions compared with the spring survey period. Hunting pressure also varied seasonally with certain hunting units being closed to game mammal hunting during the fall survey period (Fig. 1). We also chose to include the combined dataset of both seasons (henceforth referred to as 'combined') for comparison, as a vast majority of SDM studies use aggregated datasets across biologically relevant time intervals (e.g., seasons) or over multiple years. Using the combined dataset, we wanted to address how the predicted distribution from that dataset might differ from the seasonal models. Each of these partitioned datasets (spring, fall, combined) were used to construct separate distribution models of pig relative abundance.

Environmental and climate data

Environmental and climate data used in the modeling process were chosen based on the expected ecological requirements of wild pigs and the influence of anthropogenic features (Risch et al. 2020). In total, eight environmental features were used to create sets of covariates (hereafter referred to as "covariate sets") that individual

species distribution models were constructed from (Wenger and Freeman 2008). These environmental features were vegetation density, vegetation height, mean annual rainfall, elevation, native vegetative cover, distance to ungulate exclusion fences, distance to hiking trails, and distance to forest. We used data obtained from the State of Hawai'i's Office of Planning, United States Geological Survey (USGS) Gap Analysis Project (Gergely and McKerrow 2013), the Rainfall Atlas of Hawai'i (Giambelluca et al. 2012), and other layers (ungulate exclusion fences and hiking trails) provided by the Hawai'i Department of Land and Natural Resource (DLNR) Division of Forestry and Wildlife (DOFAW).

Distance and density-related variables (native cover, distance to ungulate exclusion fences, distance to hiking trails, and distance to forest) were manually generated from existing base features: USGS GAP Land Cover (30 m × 30 m), ungulate exclusion fence polygon (DLNR), and Nā Ala Hele trail system (DLNR). To generate distance-related covariates, base features were rasterized from their original resolution to 500 × 500 m and resampled using the method "majority" (Morelle and Lejeune 2015). All spatial layers used in the analysis were standardized at 500 × 500 m resolution as this was determined to be a reasonable estimate of the mean home range size for feral pigs in Hawai'i and would allow each survey location to be spatially independent (Salbosa and Lepczyk 2009; Risch et al. 2020). Distance-related variables were then created from these layers using the Euclidean distance tool in ArcGIS Pro (Version 2.7.0 Redlands, CA: Environmental Systems Research Institute, Inc. 2021). The distance to forest predictor layer was generated using only mesic and wet forests as the base layer (USGS GAP Land Cover) was unreliable in distinguishing between dry forests and sparse dry shrubland. A density-related variable (native cover) was created by masking USGS GAP Land Cover data to any vegetative cover classified as "native" and resampling the base feature (30 × 30 m) to 500 × 500 m using the method "bilinear" in the raster package 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). Collinearity between predictors was considered using pairwise Pearson coefficients and any predictors with relation > 0.75 were removed from the modeling process (Elith et al. 2010; Dormann et al. 2013).

Species distribution modeling

Species distribution models for each partitioned dataset (spring, fall, combined) were constructed using the

abundance data described above as the response variable and different configurations of the environmental covariates (referred to as “covariate sets”) as predictors in a stepwise model fitting process (Wenger and Freeman 2008; Risch et al. 2020). 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; Risch et al. 2020). Dispersion can be defined as more variance than might be expected based on mean–variance scaling and is often present in count data due to the inherent heterogeneity of biological data (e.g., detection probability) (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 environmental covariates can be included to explain the unexpected variance. Camera data were fitted to Poisson and negative binomially distributed GLMs (Poisson or NB) from the stats and MASS packages (Venables and Ripley 2002) in R (R Core Team 2019) and zero-inflated mixture models (ZIP or ZINB) with the same distributions from the pscl package (Zeileis et al. 2008) to account for issues of over or under-dispersion (White and Bennetts 1996; Martin et al. 2005; Wenger and Freeman 2008; Sileshi et al. 2009; Opperl et al. 2012; Dénes et al. 2015; Lyashevskaya et al. 2016). Zero-inflated models were included in the modeling 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 and imperfect detection (Martin et al. 2005).

Covariate sets were constructed based on a priori hypothesis of response–covariate relationship (Wenger and Freeman 2008). Given the number of survey locations, each covariate set included a maximum of three covariates used to build each respective model (see Table 1 for a sample of the best-fit covariate sets). Up to two additional covariates were included for the zero component when the data were fitted to zero-inflated models. Each covariate set was fitted to models of increasing complexity (Poisson, NB, ZIP, ZINB) until dispersion was appropriately accounted for and model overfitting was not present (Risch et al. 2020). Predicted model outputs were visually assessed for any indication of predictor overfitting (Elith et al. 2010). Covariate sets were constructed to consider first and second order relationships of each covariate used in model building and to explore interactions between covariates. The same covariate sets

Table 1 A sub-sample of the larger covariate sets including the best-fit covariate sets for spring, fall, and combined observations

Covariate set	Covariates	
	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

The zero-component terms, for covariate 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. *indicates the inclusion of an interaction between model covariates

were used to identify best-fit models for the spring, fall, and combined data (Table 1). 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; Zuur et al. 2009; Cox 2018). The dispersion parameter (φ) is calculated using Eq. 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, p. 226). Models with a dispersion parameter exceeding 1.5 were considered over-dispersed and those with much less than 1.0 were considered under-dispersed (Zuur et al. 2009). These models were either corrected for dispersion by fitting a different distribution (Poisson or negative binomial), model type (GLM or zero-inflated) or else not considered for selection as best-fit models. Best-fit models were then used to predict wild pig abundance at an island-wide scale. Model outputs were predicted across the entirety of Maui despite some areas being fenced and ungulate-free:

$$\varphi = \frac{\sum_i^n \varepsilon_i^2}{n - p}. \quad (1)$$

Seasonal differences in distribution and abundance

To identify differences in model outputs across each of the best-fit temporally scaled models, we compared the predicted abundances from each best-fit model (spring, fall, and combined). In doing so, we wanted to identify the direction and magnitude of change in predictions from each of the models. First, assuming a stable wild pig population, we standardized each of the three model outputs on a scale of 0 to 1 by dividing each of the model outputs by their respective max values using the “raster” package in R software. We then separately stacked each of the seasonal models with the combined model to identify all areas where there was either an increase, decrease, or no change in relative abundance in comparison to the

combined model or the opposing seasonal model. Further, to identify differences in abundance across landcover types for each model, we aggregated the abundance estimates by landcover type and tested for significance using the Kruskal–Wallis test (Kruskal and Wallis 1952). This process was repeated for all pig abundance estimates that fell within areas with seasonal hunting closures (Fig. 1) to identify differences in landcover use with varying hunting pressure.

Results

Model outputs

Across all temporal models, estimates of relative abundance for wild pigs varied throughout the entirety of their range. We found that annual rainfall, vegetation height, vegetation density, elevation, and distance to forest were all significant covariates in predicting wild pig abundances at different times throughout the year (Fig. 2). Annual rainfall and vegetation height were found to be the best predictors of wild pig abundance for the spring model while elevation and vegetation height were the best predictors of wild pig abundance for the combined model (Fig. 2). Annual rainfall had a significant negative model coefficient for the spring model, indicating a decrease in pig abundance with increasing amounts of rainfall (Fig. 2). In contrast, vegetation height had a significant positive model coefficient for both the spring and combined model, indicating an increase in pig abundance with increasing vegetation height (Fig. 2). Vegetation height was also found to be a significant predictor for the zero-component of the spring model and a non-significant predictor for the zero-component of the combined and fall models. Vegetation height had a negative model coefficient for the zero-component of all models indicating that with increasing vegetation height the probability of false zeroes decreased.

Aside from the influence of vegetation height on false zeroes, none of the environmental covariates that were significant predictors for the abundance of pigs in the spring and combined model performed well for the fall model. Instead, vegetation density and distance to forest were found to be the most significant covariates in predicting pig abundances for the fall model. Both vegetation density and distance to forest had significant negative model coefficients indicating a decrease in pig abundance with increasing vegetation density and distance to forest. Although vegetation height was not found to be

significant for predicting the probability of false zeroes, it was included in the fall model as AIC and dispersion values indicated better fit with its inclusion.

Models were constructed based on a priori understanding of the ecological requirements of wild pigs and AIC and dispersion values show that our chosen models performed well (Table 2). Based on AIC, GLMs with negative binomial distribution (GLMNB) performed marginally better than negative binomially distributed zero-inflated (ZINB) models (Table 2). However, the ZINB models tended to result in lower, more acceptable dispersion values and upon visual inspection of model outputs the ZINB models had less overfitting issues to environmental covariates. Both GLMs and zero-inflated models with Poisson distributions performed poorly when compared to GLMNBs and ZINBs. For the spring, the ZINB model with covariate set C was chosen due to its acceptable dispersion value and overfitting issues exhibited by the four models with lower AIC values. For the fall, the ZINB model with covariate set D was chosen despite marginally higher AIC as the visual inspection revealed the ZINB model to produce more acceptable model outputs with no signs of overfitting. Similarly, the ZINB model with covariate set B was chosen over the GLMNB for the combined dataset as the ZINB model resulted in a dispersion value closer to 1.

Seasonal differences in distribution and abundance

Differences between seasonal models and seasonal to combined models show temporal shifts in both distribution and abundance of pigs across the island of Maui throughout the year (Figs. 2, 3, 4 and 5). Differences from spring to fall show widespread decreases in pig abundance across large portions of the island with high elevation areas dominated by shrublands showing increases in pig abundance in the fall (Figs. 2, 3 and 4). The same is evident between the spring and the combined model with more noticeable decreases in predicted pig abundances in lower elevation areas and increases in abundance in higher elevation areas (Fig. 3). However, when comparing the fall to the combined model the differences are more marginal. We see only slight decreases in pig abundance throughout the lower elevation areas when comparing the fall model to the combined model and these differences are more likely a result of variance in the model predictions (Figs. 3 and 4). Many areas appear to show no change in predicted abundances between the

(See figure on next page.)

Fig. 2 Best-fit distribution models for each dataset (spring, fall, and combined) and their corresponding response curves for the set of covariates used to build each best-fit model. The two top-most response curves for each model represent the count (i.e., abundance) component of the zero-inflated model. The bottom-most response curve for each model is the probability of false zeroes as predicted by the environmental covariate used in the zero-component of the model. Estimates, standard errors (SE), and the *p-values* for each covariate used in the best-fit model are displayed on the response curve plots. All black dots represent a single abundance estimate for each 500 × 500 m cell

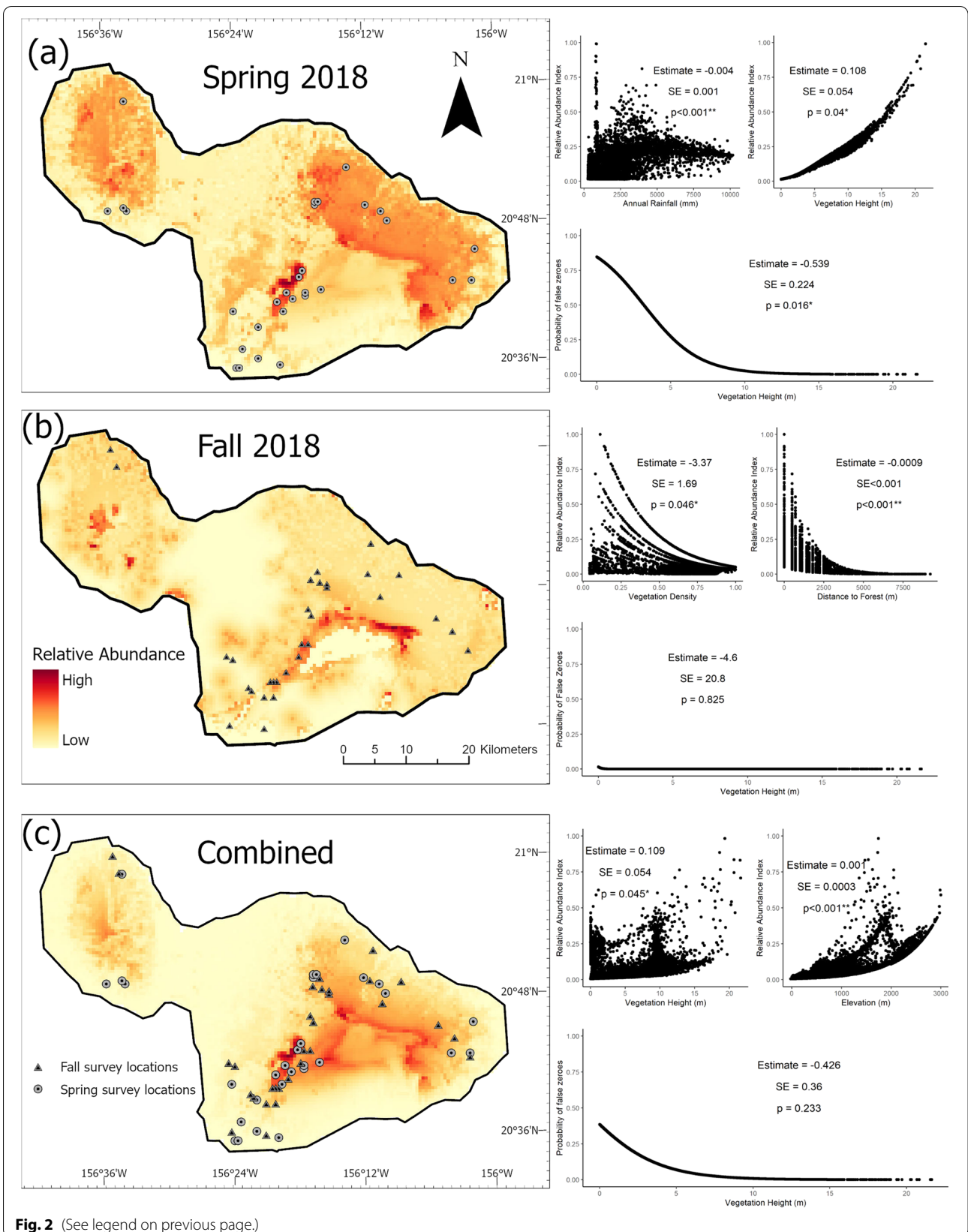


Fig. 2 (See legend on previous page.)

Table 2 Results of the top five best-fit models for spring, fall, and combined data. A breakdown of covariate set configurations can be found in Table 1

Data	Model	Covariate set	AIC	Δ AIC	ϕ
Spring	ZINB	B	196	0	1.00
Spring	GLMNB	D	196	0	0.77
Spring	GLMNB	B	198	2	0.89
Spring	ZINB	D	199	3	0.83
Spring*	ZINB*	C*	203*	7*	1.08*
Fall	GLMNB	D	240	0	1.24
Fall*	ZINB*	D*	241*	1*	1.24*
Fall	GLMNB	B	244	4	1.24
Fall	GLMNB	C	246	6	0.71
Fall	ZINB	A	247	7	0.90
Combined	GLMNB	B	446	0	1.29
Combined	GLMNB	D	448	2	1.44
Combined*	ZINB*	B*	448*	2*	1.25*
Combined	ZINB	D	452	6	1.39
Combined	GLMNB	A	452	6	0.78

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

fall and combined model; however, changes in predicted pig abundances at high elevation areas are more nuanced between these two models, particularly on east Maui. The abundance of wild pigs significantly differed by landcover type across the seasonal model outputs (Fig. 4). Wild pigs were significantly more abundant in forested areas in the spring compared to the fall and significantly less abundant in shrublands (Fig. 4). Similarly, wild pigs were significantly more abundant in forested areas when hunting was open in the spring (Fig. 5). However, when hunting was closed in these same units, wild pigs were predicted to be significantly less abundant in forested areas and significantly more abundant in both shrublands and grasslands (Fig. 5). Generally, pigs appear to utilize unique core areas at different times throughout the year and shift from one core area to another depending on season.

Discussion

By identifying differences in wild pig distribution and abundance between seasons, our study highlights the importance of separately modeling a species distribution over biologically relevant time intervals (Schurr et al. 2012; Schliep et al. 2018). Best-fit models for spring and fall show a change in abundance and distribution of wild pigs between seasons, indicating a potential shift in habitat-use or resource selection from predominantly forested areas in the spring to more open cover types

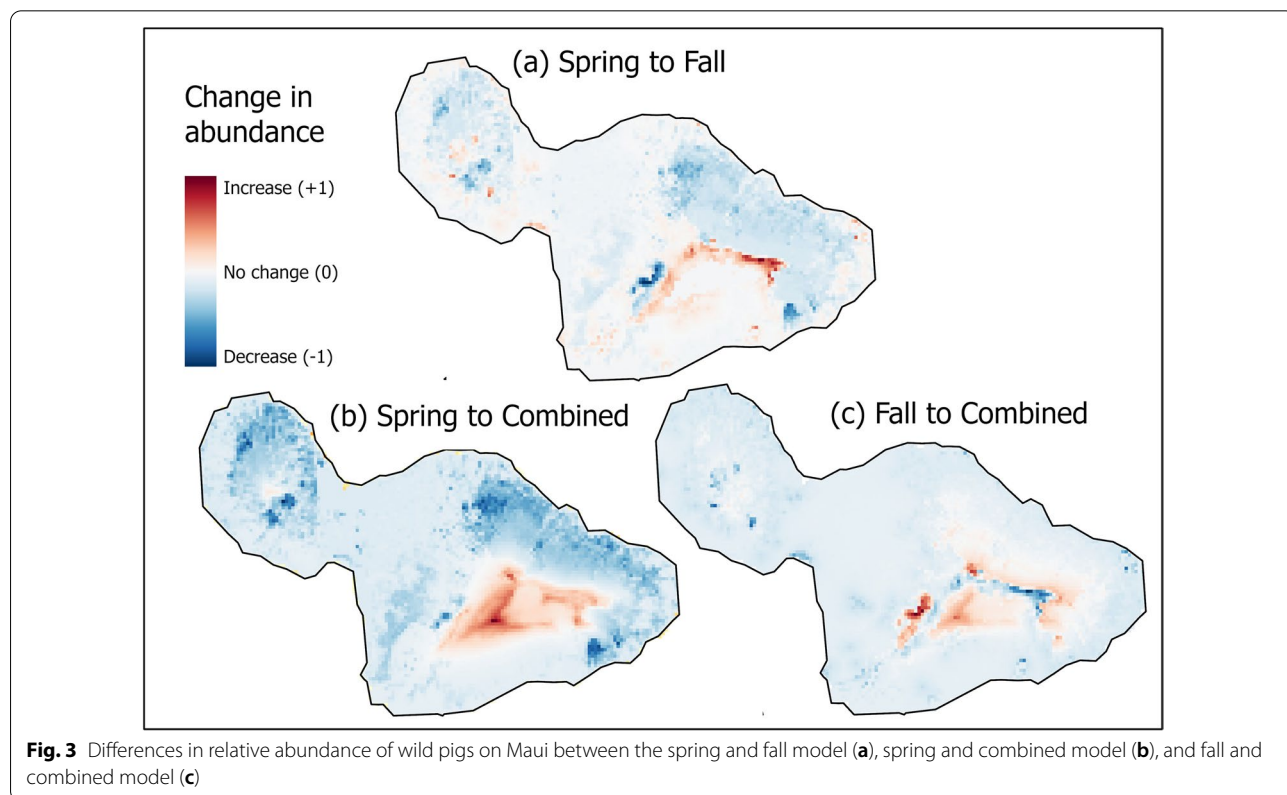
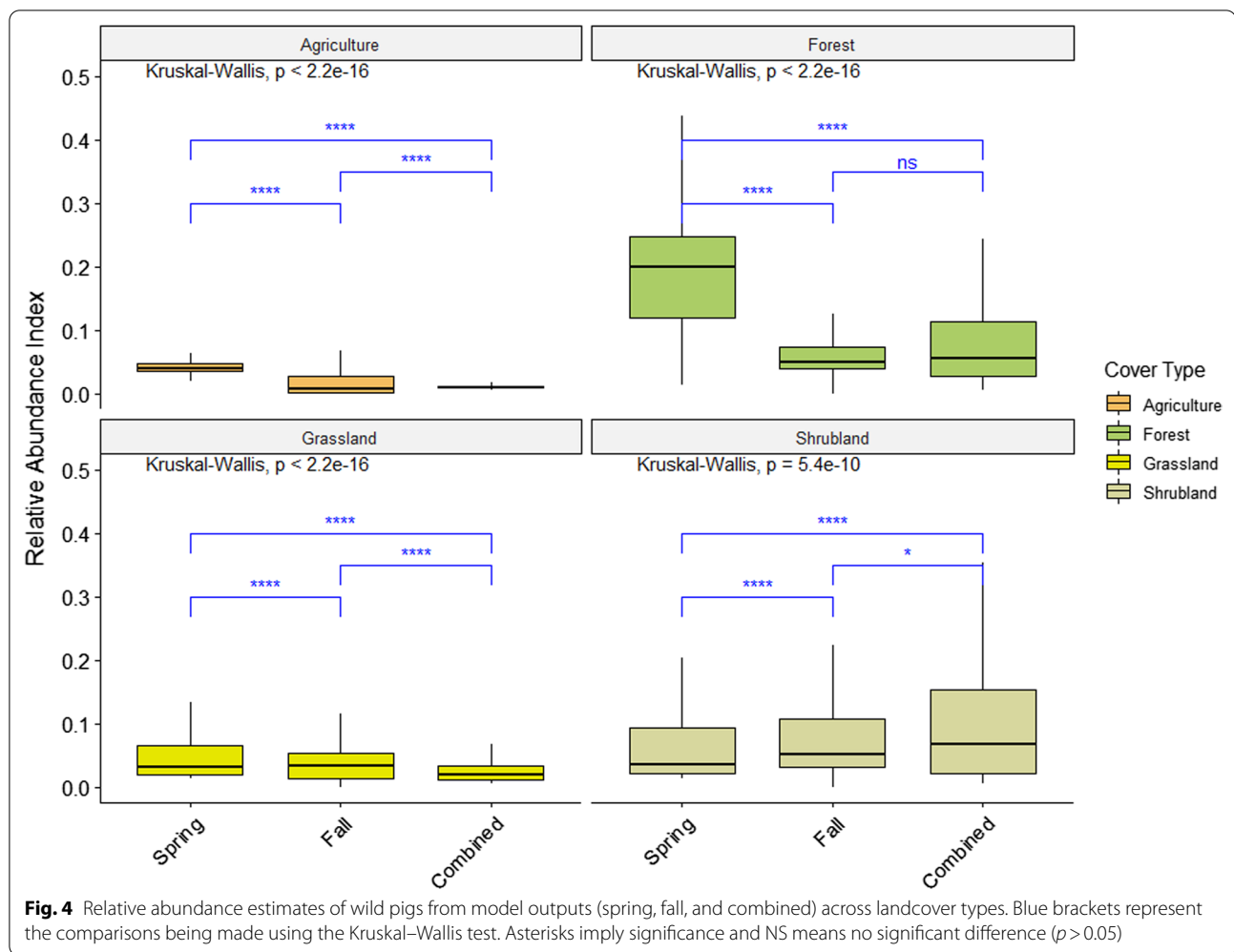


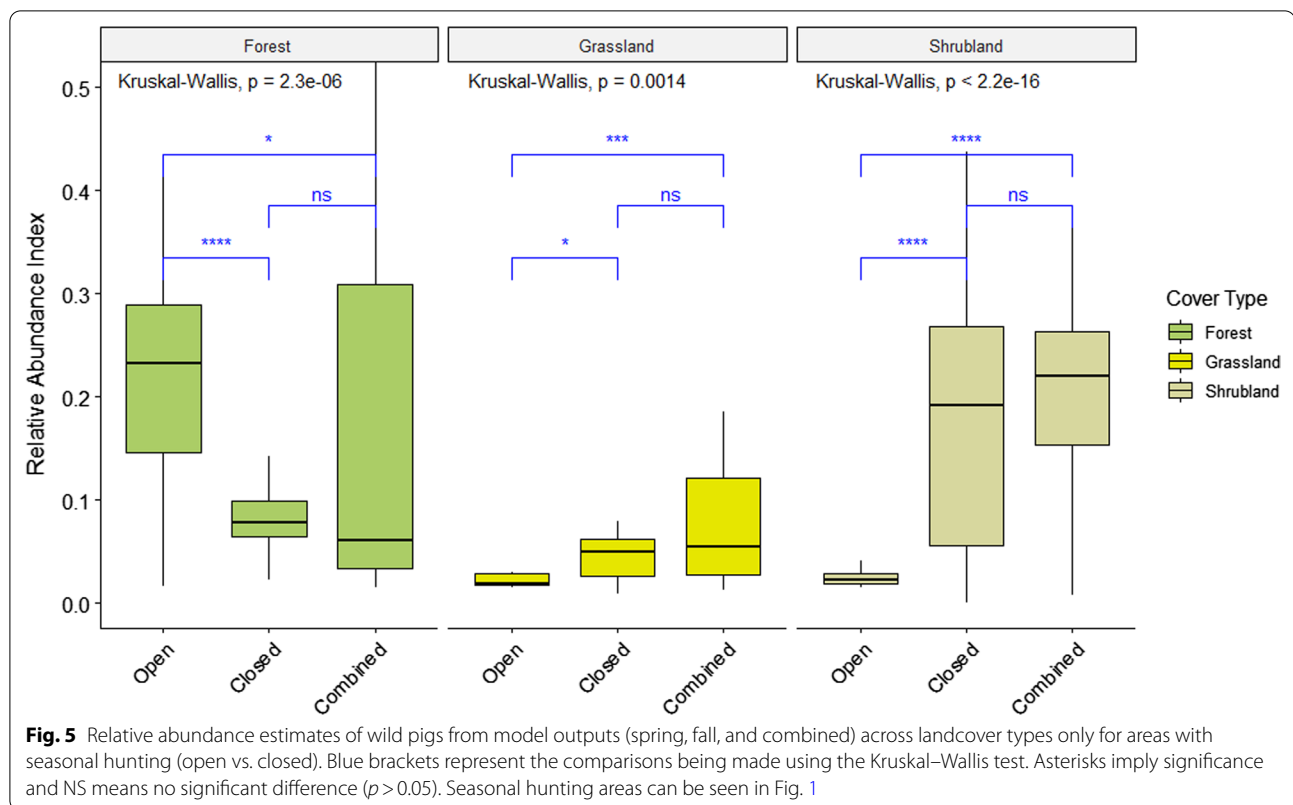
Fig. 3 Differences in relative abundance of wild pigs on Maui between the spring and fall model (a), spring and combined model (b), and fall and combined model (c)



(e.g., shrublands) in the fall. The spring and combined models identify amount of rainfall, height of vegetation, and elevation as predictors for the abundance of wild pigs. Spring and combined model results suggest that pigs are largely abundant throughout forested areas with tall mature trees, often comprising non-native species introduced from continental systems such as Cook pine (*Araucaria columnaris*), Sugi pine (*Cryptomeria japonica*), numerous eucalyptus (*Eucalyptus* spp.), and Albizia (*Falcataria moluccana*). These results are consistent with both continental and island studies that found forested habitats were commonly selected by wild pigs (Bratton 1975; Giffin 1978; Fonseca 2007; Rodrigues et al. 2016). Previous studies suggest that these areas may offer protection from human disturbance, provide thermal refuge from both hot and cold climates, and contain abundant sources of food (Merli and Meriggi 2006; Thurffell et al. 2009).

All state-managed hunting units were open for both game mammal and game bird hunting during the spring

survey period, while several units were closed for game mammal hunting during the fall survey period. 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 (Mysterud and Østbye 1999; Merli and Meriggi 2006; Stankowich 2008). While there are no natural predators of wild pigs in the Hawaiian Islands, the hunting of wild pigs is a common recreational activity (Duffy and Lepczyk 2021; Luat-Hū'eu 2020). While hunting was open in seasonal units, pigs were significantly more abundant in forested areas that presumably provided cover and protection from human disturbance (Merli et al. 2017). Conversely, when hunting was closed in these same areas in the fall, pigs were significantly more abundant in areas characterized by open cover (shrublands and grasslands) and significantly less abundant in forested areas, indicating behavioral changes as a direct result of hunting pressure.



The spring survey period coincided with the latter half of the fruiting season for many plant species commonly consumed by wild pigs. Common guava (*Psidium guajava*), strawberry guava (*Psidium cattleianum*), and banana poka (*Passiflora tarminiana*), all of which are introduced pest species, are widely abundant throughout low-to-mid elevation forested areas in the Hawaiian Islands and exhibit peak fruiting from around December to April (Giffin 1978; Stone et al. 1992). While peer-reviewed research on the relationship between these fruiting species and the distribution of wild pigs is limited, both hunter interviews (Luat-Hū‘eu 2020) and previous dietary analysis (Diong 1982) suggest pigs are drawn to fruiting areas in Hawai‘i. Our results presented here provide further empirical evidence that fruiting may drive seasonal patterns in the distribution of wild pigs.

Further, our results suggest that during the spring period and in areas of higher hunting pressure throughout the year, forested areas with tall mature trees play a crucial role in supporting abundant populations of wild pigs in tropical and sub-tropical environments as they offer refuge from human disturbance and abundant sources of food. The fall model underscored the importance of vegetation density, distance to forest, and height of vegetation as predictors for abundance of wild pigs. Although pigs were found to be most abundant in areas

with moderate to low vegetation density in the fall, the distance to surrounding forests was a significant environmental covariate, with higher abundance closer to forests, suggesting pigs were still utilizing these habitats as a source of refuge (Fig. 2). Our fall model results indicate a severe decline in the abundance of wild pigs at distances greater than 2000 m from a forested environment (Fig. 2), with the greatest abundances occurring just on the periphery of forested areas, suggesting forest edge effects (Yahner 1988).

Results from the fall model show a markedly different distribution of wild pigs compared to the spring model and generally predicted wild pigs to be more abundant at higher elevations that comprise a higher proportion of threatened and endangered species than some of the non-native forested habitats predicted by the spring and combined models (Additional file 1: Fig. S1). Wild pigs are known to frequent these high elevation sub-alpine shrublands despite an apparent lack of food resources and cover (Giffin 1978). It is presumed that wild pigs forage on small ferns or roots in these environments, which may provide an additional source of food when fruits found in adjacent forested environments are out of season (Giffin 1978). In contrast to both of our seasonal models, our combined model predicted pigs to be abundant at alpine habitat nearing the summit of Haleakalā

National Park and was the only model to show no elevational threshold for pig abundance (Additional file 1: Figs. S1). Despite Haleakalā National Park currently being fenced and ungulate-free, it is highly unlikely that the alpine habitat found near the summit would have supported any number of pigs prior to the construction of the fence due to the cinder desert being largely devoid of palatable vegetation. In this case, the combined model may have performed poorly due to inherent differences between seasonal detection rates and an inability of the model to accurately quantify these differences.

The differences in environmental covariate importance and the resulting distribution maps produced from the seasonal and combined models show a need to incorporate biologically relevant time scales in a distribution modeling framework. Incorporating relevant temporal scales (often excluded from species distribution modeling) is a crucial step to providing the most reliable and robust information to develop optimal management strategies (Elith et al. 2010; Schliep et al. 2018). These differences throughout time have important implications for management of any species of interest, but especially for those at non-equilibrium (Elith et al. 2010).

In our case, areas of increased conservation value at high elevations on Maui experienced an increase in the abundance of wild pigs during the fall, potentially threatening numerous threatened and endangered species. These areas provide some of the last remaining critical habitat to a wide variety of threatened and endangered species including several critically endangered birds and numerous plants and invertebrates (United States Fish and Wildlife Service 2016). While traditional annual or aggregate based modeling methods may have identified the threat to these areas, the seasonal change in magnitude of the threat might have been underestimated. The opposite may also hold true for our seasonal models, where survey locations with the largest differences in pig abundance may have influenced model predictions at an island-wide scale leading to an overestimate of shifts in abundance in areas that were not surveyed. However, this is an inherent limitation of modeling efforts and should be thoroughly examined in relation to known species behaviors in any distribution modeling study. Nonetheless, our models identify the months when these range shifts occur and may be used to more effectively design conservation strategies to mitigate the seasonal increase in threat from wild pigs to critical areas. As conservation resources are often limited, efforts to prioritize where conservation resources are focused are becoming increasingly important (Wilson et al. 2006). In this case, knowing that critical habitat for threatened and endangered species may be more threatened by wild pigs during the fall than the spring (or vice versa) allows conservation

efforts to be redirected to areas deemed most vulnerable and ultimately improving cost-effectiveness of conservation efforts.

Seasonal abundance information can also help inform the management of wild pigs as a game species, including opening or closure of hunting units, hunting season dates, and restrictions (e.g., hunting method or bag limit). Improved game management strategies may not only positively influence game management objectives (e.g., hunter satisfaction, food security, economic revenue), but will also likely have desirable secondary effects to conservation goals and agriculture production. In our case, we identified that within areas that undergo seasonal hunting closures, the lack of hunting pressure in the fall likely caused a significant shift in wild pigs from non-native forested areas into more open native shrublands and grasslands that also provide critical habitat for threatened and endangered species. From a game management perspective, maintaining year-round hunting in these hunting units may be mutually beneficial by providing additional hunting opportunities and reducing seasonal threats from wild pigs to critical habitat. Finally, targeting undesirable frugivorous plants shown to bolster wild pig populations and influence their distribution may provide an indirect approach to pig population control with typically lower time and resource investment than direct methods of pig removal (Beasley et al. 2018).

This study is the first to our knowledge to explicitly incorporate biologically relevant time intervals in a relative abundance modeling framework and identify seasonal trends in the abundance and distribution of a large omnivorous mammal. In this case, we observed a general trend of wild pigs moving from predominantly forested areas in the spring to more open shrubland and grassland areas in the fall. It is likely that a combination of reduced hunting pressure, changes in environmental conditions, and a lack of available food sources drove this shift. It may also be likely that survey locations that fell within areas of varying hunting pressure may have disproportionately affected overall model outputs thereby influencing estimates in areas with constant hunting pressure. However, since model results could be largely explained by known species behaviors, trends identified in this study are likely reliable. Further, model results from our combined dataset indicated a failure to accurately predict wild pig distribution in certain key areas despite model evaluation statistics indicating good fit. Future studies examining these influences on model outputs at finer spatial scales over longer periods of time are desperately needed. By separately modeling the seasonal distribution and abundance of wild pigs in a single calendar year, we were able to provide high-resolution information on seasonal movement

patterns as well as identify core areas that host high abundances of wild pigs. Biologically relevant temporal scaling of data used as inputs for distribution modeling is increasingly discussed in the literature yet is still not widely adopted in most distribution modeling efforts (especially for those using historical data gathered over multiple years) (Elith and Leathwick 2009; Schurr et al. 2012; Schliep et al. 2018). Our results highlight the importance of considering biologically relevant temporal scales and the implications they have on resulting management recommendations. This approach may not only improve model reliability it also provides essential information in the development of effective management plans to mitigate impacts of invasive species, prioritize conservation of at-risk species, and reduce risk of human–wildlife conflicts. For the appropriate management of any species, it is imperative to incorporate a thorough understanding of species ecology as it relates to both space and time. We hope that the approach presented in this study may shed light on the utility of incorporating biologically relevant time intervals and spur further discussion on the inclusion of appropriate spatial and temporal scales in future modeling efforts.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-022-00395-9>.

Additional file 1: Abundance estimates across the island of Maui from each of the best-fit models plotted against elevation.

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Author contributions

DRR, SH, and MRP conceived of and developed the project concept. DRR, MRP, and SH directed and supervised field work. DRR compiled and analyzed field data. DRR, MRP and SH verified analytical methods and interpretation of results. DRR drafted the manuscript and designed figures. All authors discussed the results, commented on the manuscript, and were involved in the writing of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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