Socio-ecological factors shape the distribution of a cultural keystone species (bearded pig, *Sus barbatus*) in Malaysian Borneo

Authors

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Abstract

Biophysical and socio-cultural factors have jointly shaped the distribution of global biodiversity, yet relatively few studies have quantitatively assessed social and ecological influences on wildlife. Drawing on a dataset of 321 total camera traps locations and 38,017 camera days across 18 field sites and three years in Sabah and Sarawak, Malaysian Borneo, we fitted occupancy models incorporating socio-cultural covariates and environmental covariates associated with bearded pig (*Sus barbatus*) occupancy. We find that all competitive occupancy models included both socio-cultural and ecological covariates. Moreover, we found that Indigenous ethnicity mediated the effect of hunting accessibility on bearded pig occupancy: Indigenous ethnicity was positively associated with pig occupancy in areas of low hunting accessibility, and negatively associated with pig occupancy in areas of high hunting accessibility. These results suggest that bearded pig populations in Malaysian Borneo should be managed with context-specific strategies, promoting Indigenous pig hunting rights in areas of low hunting accessibility. We also provide important baseline information on bearded pig occupancy prior to the 2020-2021 outbreak of African Swine Fever (ASF), which has caused social and ecological concerns after mass dieoffs of bearded pigs in Borneo, and domestic pigs across much of Asia.

Introduction

Management of socio-ecological systems must accommodate both human needs and wildlife persistence (Kays et al. 2016). Socio-cultural and biophysical landscapes are fundamentally connected, but our empirical understanding of the links between them is still limited. While researchers often quantitatively examine links between biophysical factors and wildlife, far less quantitative work has been carried out the influence of socio-cultural factors on wildlife distributions. Yet socio-cultural factors—such as ethnic identity, culturally-distinctive hunting practices, armed conflict, recreation, feasts, traditions, and value systems—have been shown to have far-reaching implications for animal behavior, wildlife distributions, and conservation efforts (e.g., Heberlein & Ericsson 2006, Wong et al. 2009, Riley 2010, Gaynor et al. 2016, Kurz et al. 2021). As such, social and cultural practices, tolerances, affinities, and other socio-cultural factors require more attention as important predictor variables, alongside ecological variables, for determining occurrence patterns of many wildlife species (Karanth et al. 2009).

A primary challenge has been integrating nuanced quantitative measures of socio-cultural factors into wildlife distribution modeling. Recently, socio-cultural covariates have begun to move beyond broader indices of human disturbance or footprint (e.g. Barber-Meyer et al. 2013, Linkie et al. 2013) to include culturally-shaped metrics, such as hunting accessibility, social carrying capacity for development, or religious practices (e.g., Bettigole et al. 2014, Stahlecker et al. 2017, Deith & Brodie 2020). These more recently adopted metrics reflect an emerging understanding of the conceptual complexity of human-wildlife interactions, which take place within nested social and ecological systems (Lischka et al. 2018). While the number of socio-ecological studies has increased dramatically in recent years (Guerrero et al. 2018), greater attention is needed to the integration of social and ecological variables in wildlife modeling (Behr et al. 2017). However, relatively few robust case studies have leveraged the social and environmental data needed to quantify their influence on species distributions.

The bearded pig, *Sus barbatus*, is an ideal species for assessing the relative contribution of socio-cultural and ecological variables to wildlife distributions. Bearded pigs are sensitive to social factors, such as hunting practices and agricultural uses (e.g. oil palm plantations, which provide supplemental food and shape bearded pig demography) (Bennett et al. 2000, Love et al. 2018, Davison et al. 2019, Kurz et al. 2021). The bearded pig is also the most favored terrestrial game species for many non-Muslim Indigenous communities in Sabah and Sarawak, accounting for up to 54-97% of their wild meat (Bennett et al. 2000, Chin 2001). Within these communities, the bearded pig is still hunted using both historical approaches (e.g. dogs and spear) and contemporary methods (e.g. on foot with a gun) (Kurz et al. 2021). Moreover, the species plays a central role in a variety of Indigenous ceremonial practices and celebrations (Janowski 2014), and it is also hunted for pest control, sport, and sale (Kurz et al. 2021). In Sabah and Sarawak, the largest Indigenous pig-hunting group makes up roughly 21% and 29% of the total population of each state, respectively (Malaysian Department of Statistics 2011), accounting for a substantial proportion of the population of each state.

In our study area, bearded pig hunting has been a particularly salient cultural force for thousands of years (Harrisson et al. 1961, Kurz et al. 2021). This hunting relationship is given further texture by the role of religion in shaping cultural affinities toward bearded pigs. In Sabah and Sarawak, religion and ethnicity are closely linked; according to census data, 100% of Malays in both states are registered as Muslim, and roughly 75% of Kadazandusun-Muruts and Ibans (the primary pig-hunting Indigenous groups in Sabah and Sarawak, respectively) identify as Christians (Malaysia Department of Statistics 2011). Wild pork is highly favored by Christian

KDM and Iban communities in Sabah and Sarawak (Bennett et al. 2000, Kurz et al. 2021), but actively avoided in Muslim communities in Malaysia generally (Yusof et al. 2012). Therefore, the role of bearded pig hunting in contemporary Malaysian Borneo also speaks to the role of religion in shaping socio-ecological interactions. Given these dynamics as well as the potential threat to pig populations posed by hunting (Bennett et al. 2000, Luskin et al. 2018), it is critical to better understand how ethnicity, and religious factors tied to ethnicity, may be related to hunting pressure and bearded pig distributions in Malaysian Borneo. It is also critical to understand the role of hunting accessibility on bearded pig distributions, as landscape resistance and social hunting norms are likely to influence the hunting pressure experienced by the species (Deith & Brodie 2020). Considering the long history of sustained pig hunting in Sabah (Medway 1964), it is possible that hunting practices in some areas may be neutral or positively associated with pig occupancies; however, human population growth, modern hunting techniques, and extensive land-use change in Sabah and Sarawak complicate this question (Bennett et al. 2000, Kurz et al. 2021).

Physical ecological factors are also likely to shape the distribution of the bearded pig. The species is dependent on forest habitat for several of its behaviors, such as wallowing, nest building, and mud scraping (Love et al. 2018). Additionally, it is thought to carry close links to Southeast Asian forest phenology due to its local and long-distance movements to track Dipterocarp fruit during mast fruiting events (Curran & Leighton 2000, Luskin & Ke 2018, Granados et al. 2019, Kurz et al. in press). However, given the logging of dipterocarps and the proliferation of oil palm plantations, it is unclear how common these nomadic movements are (Luskin & Ke 2017, Luskin et al. 2018, Kurz et al. in press). Moreover, oil palm plantations are known to provide fruit subsidies to bearded pigs (Love et al. 2018, Davison et al. 2019), raising important questions about how bearded pigs are responding to the physical environment in a context of rapid land-use change (Gaveau et al. 2016). In addition to production agricultural landscapes, the bearded pig is also adaptable to a variety of habitat types, including primary and secondary forests, mangroves, elevational gradients, and village gardens (Luskin & Ke 2017, Luskin et al. 2018, Davison et al. 2019, Kurz et al. 2021, Kurz et al. in press), allowing for comparisons across a gradient of ecological features. Finally, as the bearded pig is an IUCN-listed Vulnerable species that is vulnerable to habitat fragmentation (Luskin et al. 2018), it is important to understand the ecological correlates of pig distributions in order to develop plans for sustainable management.

Here, we integrate socio-cultural and environmental covariates to quantify their collective influence on the distribution of a cultural keystone species, the bearded pig. Selecting Malaysian Borneo as our study area allowed us to investigate socio-ecological dynamics by drawing from extensive camera trap surveys, a published hunting accessibility map, and standardized census data for Sabah and Sarawak. Drawing on an extensive camera trap dataset of 321 locations distributed across land-use, management, and socio-cultural contexts, we investigate how two key social factors—ethnicity and hunting accessibility—and how several physical environmental factors together shape bearded pig occupancy. Occupancy is a useful metric of distribution that has been frequently used to understand threatened animal distribution in Southeast Asia (e.g. Linkie et al. 2013, Nguyen et al. 2022). We run occupancy models in a multi-model framework with top models ranked by AICc. Our results: (a) provide novel empirical associations between socio-ecological factors and the distribution of a large-bodied game species; and (b) provide area-specific baseline evidence of bearded pig occupancies before the 2020-2021 African Swine Fever (ASF) outbreak. In light of these findings, we discuss the implications of our results for context-specific bearded pig management in Sabah and Sarawak.

Results

Socio-cultural and environmental factors associated with bearded pig occupancy

All top-ranking occupancy models included both socio-cultural and ecological covariates (Table 1). The socio-cultural covariates for occupancy probability included in competitive models were: hunting accessibility, proportion of Indigenous pig-hunting group, and their interaction (Figure 1, Table 1). Hunting accessibility alone was also positively associated with bearded pig occupancy (Figure 2, Table 2). The ecological covariates associated with occupancy probability in competitive models were: elevation, protected area status, slope, and tree cover. Slope was negatively associated with bearded pig occupancy (Figure 2). Distance to forest edge and distance to water were not present in the top models. Non-tree vegetation cover was negatively associated with detection probability (Table 2).

Interaction between Indigenous pig-hunting group and hunting accessibility

The interaction between the proportion of the district population composed of the predominant Indigenous pig-hunting group and hunting accessibility was significant in the model-averaged model ($p < 0.001$, Table 2). At low levels of hunting accessibility, Indigenous group proportion was positively associated with pig occupancy (Figure 1). At high levels of hunting accessibility, Indigenous group proportion was negatively associated with pig occupancy. At medium levels of hunting accessibility, the effect of Indigenous group proportion on pig occupancy was largely unchanged.

Estimated occupancy and detection of bearded pigs across study area

Our results show consistently high occupancy by bearded pigs across most forested areas studied in Sabah and Sarawak. Predicted average bearded pig occupancy (psi ± SE) across study sites in our fitted occupancy models was 0.75 ± 0.05. Predicted average bearded pig occupancy per site ranged from 0.99 ± 0.01 to 0.27 ± 0.12 (Table 3). Estimated bearded pig detection probability (p ± SE) during a 7-day survey period across study sites was 0.36 ± 0.01.

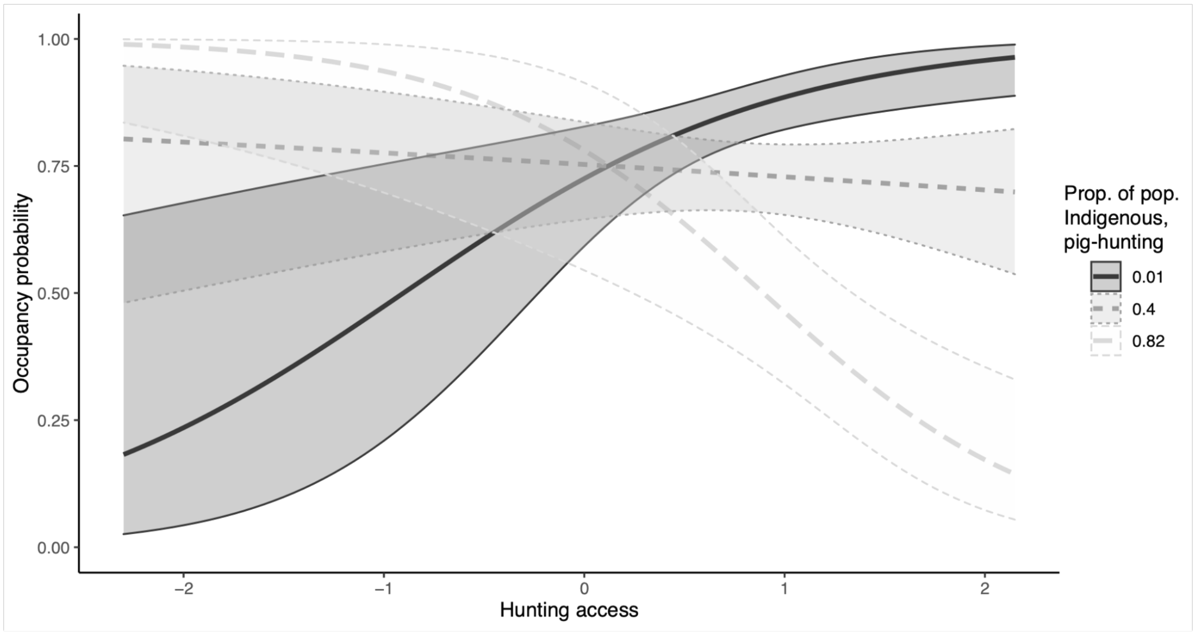

Figure 1. Interaction plot showing the relationship between hunting accessibility, proportion of predominant Indigenous pig-hunting group, and pig occupancy.

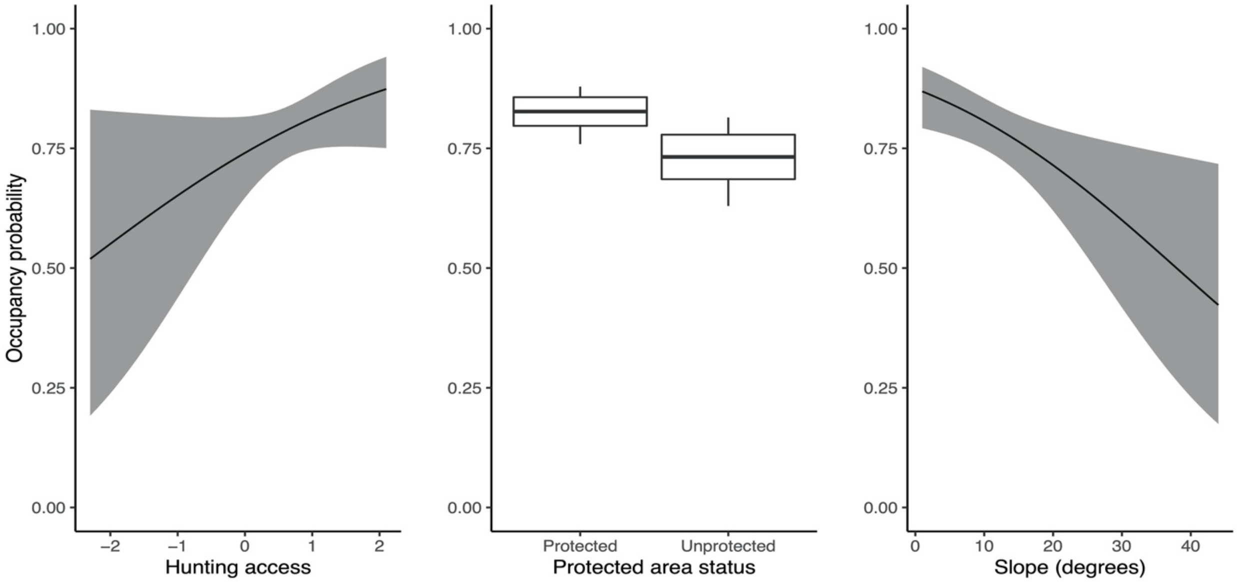

Figure 2. Added variable plots for hunting accessibility, protected area status, and slope. The plots show the relationship between the variable and pig occupancy probability, while holding other covariates constant.

Table 1. Occupancy models within <2 ΔAICc of the top ranked model; "p" indicates detection probability and "psi" indicates occupancy probability. "Model" shows the variables present in the model, "W" indicates model weight, "AICc" indicates corrected Akaike Information Criterion, and ΔAICc indicates the difference in the AICc between the model and the top model. [Covariate abbreviations are: I = Intercept; NT = non-tree vegetation cover; elev = Elevation; Ind = Proportion of district population composed of predominantly pig-hunting Kadazandusun-Murut or Iban racial-ethnic group; Acc = Hunting accessibility; Tree = Percent tree cover; PA = Protected area status; slp = Slope; Ind*Acc = Interaction of Proportion of district population composed of predominant pig-hunting Indigenous group and Hunting accessibility]

Model	W	AICc	ΔAICc
p(I) + psi(I) + p(NT) + psi(Ind) + psi(Acc) + psi(PA) + psi(slp) + psi(Ind*Acc)	0.216	5779.1	0
p(I) + psi(I) + p(NT) + psi(elev) + psi(Ind) + psi(Acc) + psi(PA) + psi(slp) + psi(Ind*Acc)	0.185	5779.4	0.32
p(I) + psi(I) + p(NT) + psi(Ind) + psi(Acc) + psi(slp) + psi(Ind*Acc)	0.120	5780.2	1.17
p(I) + psi(I) + p(NT) + psi(elev) + psi(Ind) + psi(Acc) + psi(slp) + psi(Ind*Acc)	0.082	5781.0	1.94
p(I) + psi(I) + p(NT) + psi(Ind) + psi(Acc) + psi(Tree) + psi(PA) + psi(slp) + psi(Ind*Acc)	0.081	5781.0	1.95

Table 2. Model average of models within <2 ΔAICc of the top model (See Table 2); “p” indicates detection probability and “psi” indicates occupancy probability. Coefficient estimates, standard error, and p values are listed for each variable. Significant relationships between covariates and bearded pig occupancy are denoted: *($p < 0.05$); **($p < 0.01$); ***($p < 0.001$). [Abbreviations: Elev. = Elevation; Indig. = Proportion of district population composed of KDM or Iban group; Access. = Hunting accessibility; PAs. = Protected area status; Slp. = Slope].

Variable	Est.	SE	p
p(Intercept)	-0.31	0.09	0.0006***
psi(Intercept)	1.27	0.57	0.0258*
p(Percent non-tree vegetation cover)	-0.01	<0.01	0.0012**
psi(Prop. of Indigenous pig-hunting group)	0.06	0.96	0.9510
psi(Hunting accessibility)	1.05	0.38	0.0054**
psi(Protected Area status)	0.41	0.38	0.2761
psi(Slope)	-0.05	0.02	0.0086**
psi(Prop. of Indig. group * Hunting acc.)	-3.00	0.79	0.0002***
psi(Elevation)	<0.01	<0.01	0.5280
psi(Percent tree cover)	>-0.01	<0.01	0.8994

Table 3. Estimated occupancy for bearded pigs at study sites across Sabah and Sarawak, Malaysian Borneo, prior to the outbreak of African Swine Fever in 2021. *For this site, the estimated psi value was 0.996. $^{+}$For the SAFE Project sites, the cameras located in oil palm plantations were not included due to a small sample size.

Site	Est. occupancy (psi ± SE)
Crocker Range National Park	0.51 ± 0.10
Danum Valley Conservation Area	0.85 ± 0.05
Gunung Mulu National Park	0.52 ± 0.12
Hose Mountains*	0.99 ± 0.01
Lower Kinabatangan Wildlife Sanctuary	0.91 ± 0.03
Madai Baturong	0.90 ± 0.05
Maliau Basin Conservation Area	0.90 ± 0.05
Pulong Tau National Park	0.89 ± 0.06
SAFE Project^{+} 2012	0.64 ± 0.06
SAFE Project^{+} 2014	0.79 ± 0.10
Sapulut	0.27 ± 0.12
Silabukan	0.80 ± 0.07
Sipitang	0.75 ± 0.08
Tabin Wildlife Reserve	0.84 ± 0.05
Tawau Hills Park	0.45 ± 0.08
Ulu Baram	0.92 ± 0.05
Ulu Padas	0.83 ± 0.07
Ulu Trusan	0.78 ± 0.05

Discussion

Our results provide robust, quantitative evidence that socio-cultural and ecological factors underpin the spatial distribution of a large-bodied game species. By demonstrating the importance of socio-ecological drivers in wildlife distribution modeling for this species, our approach goes beyond many conventional modeling frameworks that consider ecological factors in isolation or that use broad indices of human footprint. Furthermore, our results empirically link Indigenous groups, hunting accessibility, and bearded pig occupancy. We shed new light on these socio-ecological relationships by showing that ethnicity mediates the effect of hunting accessibility on a cultural keystone species.

Influence of hunting accessibility and Indigenous hunting practices

Socio-cultural covariates were significant predictors of bearded pig occupancy, highlighting the relevance of cultural practices—in this case, hunting accessibility—for wildlife distributions. While conceptual models of socio-ecological systems are becoming increasingly common (e.g. Lischka et al. 2018), and urban ecology has embraced human demographics and cultural practices in wildlife distribution assessments (e.g. Alberti et al. 2003, Kumar et al. 2018), we assert that it is critical to normalize more fully the integration of socio-cultural practices into wildlife ecology and conservation. In our study context, social landscapes and ecological landscapes share important intersections. Deith & Brodie (2020) show that hunter movements are strongly associated with landscape characteristics across Malaysian Borneo. Our results build on this link by showing that hunting accessibility (i.e. the potential for hunting pressure) is also strongly associated with a game species response.

The proportion of Indigenous pig-hunting population and hunting accessibility showed a strong interaction, with important lessons for socio-ecological theory and wildlife management. At low levels of hunting accessibility, Indigenous group proportion was positively associated with pig occupancy. However, at high levels of hunting accessibility, the opposite relationship was true. The role and relevance of ethnicity, including cultural practices, in empirical and theoretical studies of wildlife distribution has been too often overlooked. However, robust cultural traditions have important implications for conservation value formation (Van Houtan 2006), and social practices shape wildlife utilization patterns across the globe (Hunt & Ditton 2002, Amador et al. 2015, Kurz et al. 2021). Our findings validate this theoretical consideration by empirically demonstrating the connections between ethnicity and bearded pig occupancies in Malaysian Borneo. On a management level, this finding tracks with other studies highlighting opportunities for integration of Indigenous harvesting practices and sustainable management of game species, such as moose (Popp et al. 2019), primates (Shaffer et al. 2018), and whales (Breton-Honeyman et al. 2021). The positive relationship between Indigenous group proportion and pig occupancy at low levels of hunting accessibility suggests that there are still pathways for sustainable hunting of bearded pigs, which have been hunted in our study area for thousands of years (Harrisson et al. 1961, Medway 1964). However, the negative association between Indigenous groups and pig occupancy in high-accessibility areas highlights the need for adaptive, context-specific management and land-use planning that incorporates hunting as a land use (Neumann et al. 2022).

In our study region, ethnic identification is also tightly linked to religion, leading to additional cultural implications for bearded pig hunting. The majority of KDM and Iban communities identify as Christian (although a minority are Muslim), and the vast majority of Malays identify as Muslim (Malaysia Department of Statistics 2011). These tight ethno-religious identifications add an additional layer of group identity to pig hunting practices and dietary choices. In fact, food practices rooted in religion and ethnicity are so strong in our study area that a “pig line” has been recorded in Sarawak between Muslim fishing communities along the coast and Christian pig-hunting communities in the interior (Bolton et al. 1972). While ethno-religious traditions have been linked to harvest of wild animals and plants (e.g., Wadley et al. 1997, Golden & Comaroff 2015, Pieroni & Sõukand 2019), relatively few studies have explored these connections. Therefore, by showing the influence of ethnicity, including religious dimensions of ethnicity, on bearded pig occupancy, our findings make a compelling case for the wider relevance of cultural factors on wildlife consumption patterns generally.

Context-specific management of bearded pigs in Malaysian Borneo

Our results support context-specific management of bearded pigs in Sabah and Sarawak, Malaysian Borneo. Average estimated occupancy probabilities for bearded pigs was high, at 0.75 ± 0.05 ($psi \pm SE$). However, spatial variation in predicted occupancy, which varied widely across field sites (0.27 - 0.99), suggests a range of management needs for bearded pig populations, which are known to have widely varying movement patterns and population growth rates that correspond to different population states (Caldecott et al. 1993). Bearded pig natural history fits many characteristics of a generalist species—e.g., dietary flexibility, broad habitat use, and high dispersal ability (Luskin & Ke 2017, Davison et al. 2019)—yet the species still seems to require forest cover for safety, thermoregulation, and nesting (Luskin & Potts 2011, Love et al. 2018, Kurz et al. 2021). As such, management strategies that preserve contiguous forest areas are important, particularly in areas of low pig occupancy.

Moreover, our results show a positive (though non-significant) relationship between bearded pig occupancy and protected areas. This finding suggests that bearded pig conservation planning in Sabah and Sarawak could include a role for national parks, wildlife sanctuaries, wildlife reserves, conservation areas, nature reserves, protection forest reserves, state parks, permanent forest estates, and other protected areas. Large protected areas may also be one of the last opportunities for conserving the unique migratory ecology of bearded pigs, which are thought to historically have traveled for hundreds of kilometers tracking supraannual mast fruiting bounties (Caldecott & Caldecott 1985). Large tracts of protected forest in Borneo and Sumatra are likely the only places remaining with sufficiently high masting activity (e.g. Granados et al. 2019), intact migration corridors, low hunting risk, and reduced influence of oil palm fruit subsidies - together potentially establishing conditions for long-range bearded pig nomadic movements.

The outbreak of African Swine Fever (ASF) has led to the collapse of bearded pig populations across Sabah, and is a threat to populations in Sarawak (Kurz et al. in press). ASF case fatality rates of 47.7 to 100% have been recorded in wild and domestic pigs (Liu et al. 2020, FAO 2021). Our site-specific findings therefore provide a critical baseline of bearded pig occupancy in a number of areas within Malaysian Borneo, prior to the outbreak of ASF. As populations recover, further research can compare future bearded pig occupancy relative to baselines for specific areas as part of ongoing monitoring efforts for this IUCN-listed Vulnerable species (Luskin et al. 2018). Preserving the role of protected areas across the large spatial extent of Malaysian Borneo may also aid in the distribution of bearded pig sub-populations, allowing some individuals to escape the outbreak and providing contexts for pig populations to safely recover.

Finally, our results point to a need to manage bearded pigs to provide for sustainable Indigenous hunting practices and resilient bearded pig populations. Our results indicate that in both high and low hunting accessibility areas, there may be pathways for sustainable bearded pig hunting. In low hunting accessibility areas, we found that Indigenous groups were positively associated with pig occupancy, suggesting that customary Indigenous pig hunting rights can co-exist with sustainable management of pig populations, as they have for thousands of years (Harrisson et al. 1961). In high hunting accessibility areas, communities from non-Indigenous pig-hunting groups were positively associated with pig occupancy. Moreover, hunting accessibility generally was positively associated with pig occupancy (Figure 2). This result could suggest that pig occupancies are high in areas with more foreign workers, such as oil palm plantations which, in Sabah, can have up to 95% foreign workers from the Philippines and Indonesia (Bernard & Bissonnette, 2011). High levels of bearded pig utilization of oil palm plantations and mixed forest-oil palm landscapes have been recorded (e.g. Love et al. 2018, Davison et al. 2019), aligning with these results. Bearded pig hunting is allowed in both Sabah and Sarawak outside of protected areas and, in the case of Sabah, with a hunting license (Wildlife Conservation Enactment 1997, Wildlife Protection Ordinance 1998, Wilting et al. 2006, Yi and Mohd-Azlan 2020). Therefore, we recommend preserving Indigenous pig hunting rights while also ensuring the protection of pig populations in protected areas. In particular, regulated hunting in and around industrial and small-scale oil palm plantations could improve pest control in plantations while also providing limited hunting opportunities for KDM and Iban hunters (Kurz et al. 2021). Additionally, high pig occupancy estimates across most of our study sites and high bearded pig reproductive capacity (Luskin & Ke 2017) also suggest that balancing these goals is possible. However, further work on the dynamics between pig densities and oil palm plantations is needed before specific regulations could be most accurately developed.

Nuanced solutions will be critical so that Indigenous communities in Sabah and Sarawak can continue to sustainably hunt bearded pig populations, as they have for millennia (Harrisson et al. 1961, Medway 1964). For integrated biocultural conservation goals, it is critical to preserve the cultural and dietary importance of bearded pig hunting for Indigenous groups while also limiting hunting to sustainable levels for bearded pig populations (Kurz et al. 2021). Our results highlight the tensions and challenges of these twin goals.

The significance of density estimates for bearded pigs

Our study focused on the influence of socio-ecological factors on occupancy, and did not include density estimates within the scope of our analysis. Bearded pigs have a number of population states of varying densities under different environmental conditions (Caldecott et al. 1993), presumably resulting in varying levels of resilience to hunting pressure. In areas with plentiful food resources and high pig densities, bearded pig resilience to hunting could be high; indeed, during resource-rich mast fruiting periods, female bearded pigs can give birth to 10-30 piglets in a single year (Luskin & Ke 2018). In Sabah, older pig hunters recall pig mass movements more than younger hunters (Kurz et al. 2021); this pattern may point to fewer large-scale mast fruiting events accompanied by bearded pig herding behavior (Caldecott & Caldecott 1985; Caldecott et al. 1993). Additionally, in contemporary Malaysian Borneo, oil palm plantations provide year-round food subsidies to bearded pigs in many areas (Davison et al. 2019, Kurz et al. 2021); for example, in one mixed landscape, bearded pigs were found in 80% of oil palm transects adjacent to forest (Love et al. 2018). Therefore, the relationship between high bearded pig densities and hunting accessibility deserves further study, and could hold important implications for context-specific hunting management.

Methods

Study region and data collection

We collated bearded pig detections and non-detections from 18 camera trap surveys conducted over 2010, 2012, and 2014 across the Malaysian Bornean states of Sabah and Sarawak (Figure 3). We followed institutional guidelines for research and obtained local research permissions from the Sabah Forestry Department, Forest Department Sarawak, Sabah

Biodiversity Centre, and the Sarawak Biodiversity Centre (permit #s: JKM/MBS.1000-2/12(156) and JKM/ MBS.1000-2/2 JLD.3 (18)).

From these surveys, we integrated data from a total of 321 camera trap locations, comprising 3,613 bearded pig detections across 38,017 camera days. Camera surveys were designed to target multiple mammal species and were therefore suitable for detecting bearded pigs, one of the most common mammals in many camera surveys in our study area (e.g. Bernard et al. 2013, Mohd-Azlan et al. 2019). Within each year, we spatially filtered camera locations to ensure at least 1 km between camera stations. For studies using paired cameras at each sampling location, we applied a random number generator to randomly select one camera from the pair.

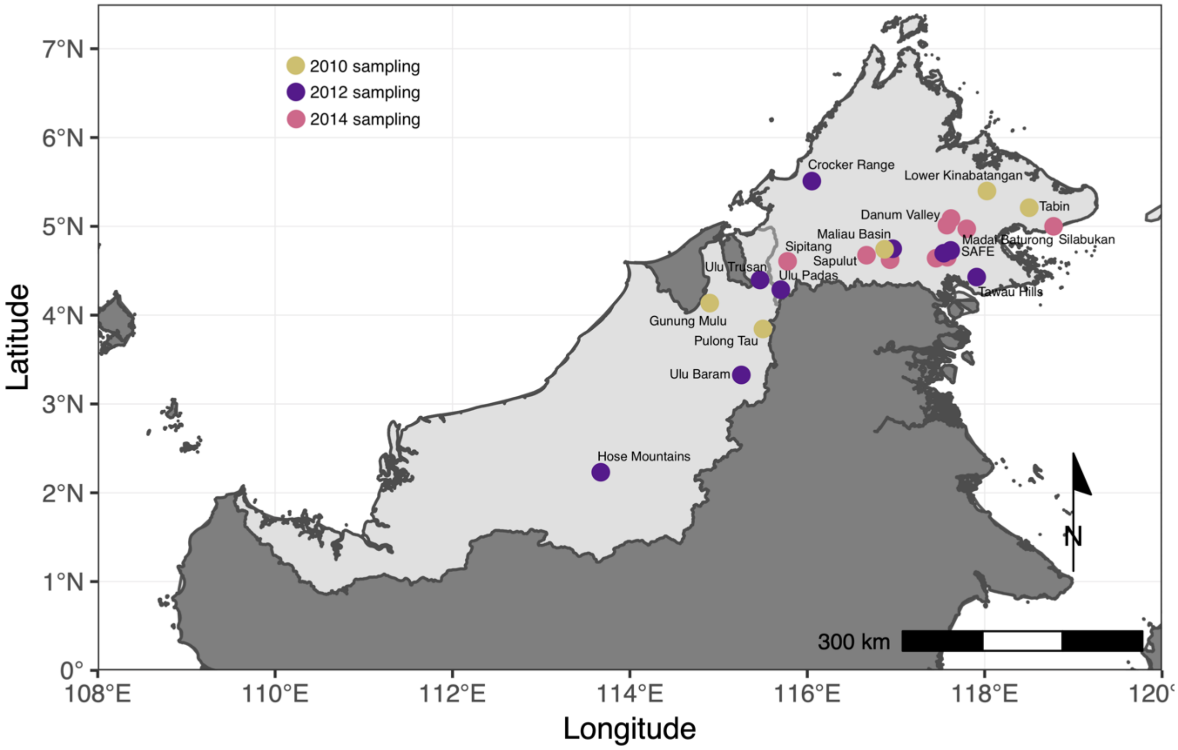

Figure 3. Location of 18 wildlife camera surveys conducted in 2010, 2012, and 2014.

Camera trap surveys were carried out within protected areas (e.g. state parks, national parks, protection forest reserves, wildlife sanctuaries, virgin jungle reserves) and non-protected areas (e.g. forest remnants, oil palm plantations). Human hunting accessibility across the study area varied considerably; our survey data included low and high hunting accessibility areas (Deith & Brodie 2020). Camera trap surveys were carried out across primary forest (lowland and montane), previously logged secondary forest (lowland and montane), and oil palm plantations

(Miettinen et al. 2012). Together these habitat types make up the majority of non-urban land cover in Sabah and Sarawak (Miettinen et al. 2016).

Within arrays, cameras were active for varying lengths of time (Supplemental Table 1), but our overall dataset spans 2010, 2012, and 2014.

Occupancy modeling approach

We chose covariates hypothesized to be strong predictors of bearded pig occupancy (Table 4). We used percent of non-tree vegetation cover as our predictor for detection. We removed highly correlated continuous covariates until Pearson's correlation coefficients among all pairs were less than |0.6| (Zuur et al. 2009, R Core Team 2019). Ecological covariates (extracted from Earth Engine Data Catalog) included in analyses were distance to water (Pekel et al. 2016), distance to forest edge (Gaveau et al. 2016), protected area status (UNEP-WCMC and IUCN 2019), elevation (Farr et al. 2007), slope (Farr et al. 2007), and tree cover (Dimiceli et al. 2015) (Table 4, Supplemental Table 2). To match environmental variables with the camera trap data, we either used the closest year of environmental data or an average of multiple years.

Table 4. Social and ecological covariates included in occupancy models. KDM is a locally-used abbreviation for the Kadazandusun-Murut Indigenous group.

Model covariate	Hypothesized relationship with occupancy	Covariate type
Hunting accessibility	—	social
KDM or Iban Indigenous group	—	social
Hunting accessibility*Indigenous grp.	—	social
Distance to water (m)	—	ecological
Distance to forest edge (m)	+	ecological
Protected area status	+	ecological
Elevation (m)	+	ecological
Slope (deg)	—	ecological
Tree cover (%)	+	ecological

The social covariates included in the models were: proportion of predominant Indigenous pig hunting group (at the district level), hunting accessibility, and their interacting effects (Table 4, Supplemental Table 2). For the racial-ethnic group covariate, we used published census data to calculate the proportion of the total district population composed of the predominantly Christian, bearded pig hunting ethnic group in each state: the KDM peoples in Sabah and the

Iban peoples in Sarawak (Bennett et al. 2000, Malaysian Department of Statistics 2011, Kurz et al. 2021). To incorporate hunting accessibility into our models, we used a published estimate of hunting pressure across Malaysian Borneo based on estimates of hunters' population densities and their expected movement through fine-scale complex habitats (Deith & Brodie 2020). While our hunting accessibility metric accounts for the relative human population in a given area (Deith & Brodie 2020), it is unable to capture cultural influences within the local population engaging in hunting in that area. A higher metric score indicates higher hunting accessibility, and vice versa (Deith & Brodie 2020). By including the proportion of Indigenous pig-hunting population in each district (including the interaction between this proportion and hunting accessibility), we attempted to incorporate the influence of local pig-hunting cultural practices into our models.

We fitted one single-season occupancy model for all the data from 2010, 2012, and 2014 (Davidson 2020). However, given the long-distance movements for which the bearded pig is known (Caldecott & Caldecott 1985, Curran & Leighton 2000, Luskin & Ke 2018), detections of bearded pigs cannot be considered independent and their populations cannot be considered closed. Therefore, model-estimated occupancy results for species in this situation should be interpreted as probability of site use rather than true occupancy (sensu Petracca et al. 2018, Gould et al. 2019).

We ran models using the package 'unmarked' (Fiske & Chandler 2011) in R version 3.6.0 (R Core Team 2019). We then used the 'dredge' function (Bartoń 2009) in R version 3.6.0 to identify top models (R Development Core Team 2019) according to Akaike's Information Criterion values, adjusted for small sample sizes (AICc). Models within a delta AICc of 2 were considered to be competing models (Ainley et al. 2006). We also model-averaged the top models within delta AICc of 2. Significance tests for variable effects were two-sided. To illustrate the influence of key variables, we created interaction and added variable plots in R version 3.6.0 (R Development Core Team 2019).

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Author Contributions Statement

JSB conceived the study. DJK, TC, and JSB designed the research approach. JFB, AH, PCG, OW, AA, ELB, HB, NJD, JGEW, AG, OH, H-YL, MSL, DM, JM-A, JR, BS, MS, and BG contributed to field work. SHZ led collation of covariates and DJK led collation of camera data. TC led the analysis, and DJK, SHZ, JFB, OW, MD, NJD, AG, MSL, MS, MDP, and JSB contributed to the analysis. DJK led writing, and all authors contributed to writing, review, and approval of the manuscript.

Competing Interests Statement

The authors declare no competing interests.

Data Availability Statement

The census data and environmental variable data used in this study are publicly available (see Supplemental Table 2). Data sharing for the camera trap data is not applicable to this study, as no new camera data were created for this study. Requests for camera data may be made to the authors of the original camera studies for which those data were collected.

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