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LETTER

The mass mortality of Asia's native pigs induced by African swine fever

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Abstract

Asia's wild pigs are ecosystem engineers and a key food for predators and people. The arrival of African swine fever (ASF) in 2018 induced near-100% fatality in domestic pigs and decimated the Chinese pork industry in 2020 but outcomes for wild pigs have been delayed and unclear. Here we report on the mass mortality of native wild boar (*Sus scrofa*) in Peninsular Malaysia. ASF was confirmed at our long-term study site in February 2022 and wild boar carcasses increased >100-fold in June 2022 compared to prior years. Camera trapping revealed an 87% decline in wild boar activity in 2022 compared to five prior surveys. Wild boars retired in old birthing nests and pairs of animals died next to each other in the open. Similar results are being anecdotally reported across the region with immense repercussions suspected on ecology and conservation. We urge a rapid research response to take advantage of this unique natural experiment.

KEYWORDS

emerging infectious diseases, prey depletion, species conservation, *Sus scrofa*, zoonotic disease

INTRODUCTION

The world's major international organizations representing food, animals, and conservation have issued a joint statement on the impending threat that the lethal onslaught of African swine fever (ASF) poses to Asia's domestic and wild pigs, ecosystems, and people (FAO et al., 2021). This follows on prior analyses suggesting ASF could threaten Southeast Asia's 11 endemic wild pig species with severe population crashes or extinction (Luskin et al., 2020). However, reports of ASF in Southeast Asia's wild pigs have been limited to isolated coincidental reports of mortality events of bearded pigs (*Sus barbatus*) in Borneo, wild boar (*Sus scrofa*) in Laos and Vietnam, and warty pigs (*Sus cebifrons*) in the Philippines (Denstedt et al., 2021; Ewers et al., 2021; FAO et al., 2021; Oberin et al., 2022). There has been little reporting on the extent of ASF in wild boar (*Sus scrofa*) from Thailand, Peninsular Malaysia, Singapore, and Sumatra, where the species is abundant—or hyperabundant—across much of the region's intact and degraded forests, including logged, fragmented, and edge habitats (Z. Amir, Moore, et al., 2022; Ickes, 2001; Khalidah et al., 2021; Lamperty et al., 2023; Luskin et al., 2017; Moore et al., 2016). The lack of documented ASF in Southeast Asia's wild boars to date has been

perplexing given their prior high densities, gregarious social behavior, and propensity to utilize human-modified landscapes increasing their proximity with domestic pigs that are ASF vectors.

ASF is a disease caused by a highly transmissible DNA virus that is spread directly through contact or consumption of infected carcasses or even cooked pork products, and indirectly via vectors such as ticks (FAO, 2021). The "Asian pig pandemic" was triggered by international trade, with ASF invading the Chinese pork industry in 2018 and causing losses exceeding $100 billion USD in 2019 and 2020 (Weaver & Habib, 2020). ASF causes near 100% fatality in Asia's domestic pigs (*S. scrofa domesticus*) and a variety of other Suidae species, but is harmless to people and other animals (FAO, 2021). However, wild native European populations of *S. scrofa* have faced multiple waves of ASF over the last two decades and show some immunity to the disease and ASF has even become endemic in some regions (Chenais et al., 2019). Therefore, the outcomes for Asia's wild native *S. scrofa* populations remain unclear.

Our team has been monitoring the population of native wild boar (*S. scrofa*) at the 130 km^2 Pasoh Research Forest in Peninsular Malaysia for three decades (Ickes, 2001; Ickes et al., 2005; Luskin et al., 2017, 2019, 2021). Pasoh is home to Asia's longest-running permanently staffed forest dynamics plot, providing the opportunity to monitor the ASF outbreak (Davies et al., 2020). The population dynamics of Pasoh's wild boars (*S. scrofa*) are closely tied to cross-boundary food subsidies provided by oil palm fruits in plantations that are adjacent to the reserve (Luskin et al., 2017). Before the incidence of ASF, Pasoh's wild boar densities were estimated at 27–47 individuals/km^2 (Ickes, 2001; Luskin et al., 2017). These densities are higher than wild boar densities in natural forests without external food subsidies (2–10 individuals/km^2) and have therefore been referred to as "hyperabundant" (Ickes, 2001). Pasoh's wild boar population declined when adjacent oil palm trees were not fruiting from 2002–2006 (Luskin et al., 2017). However, carcasses were not found during these non-fruiting periods, suggesting that the wild boars migrated from the area and did not die in large numbers from starvation. When the neighboring plantations resumed fruiting in 2007, the wild boar population increased exponentially until 2012 (Luskin et al., 2017) and remained hyperabundant through February 2022.

Here we examine the mortality dynamics of an ASF outbreak in Asian wild pig species and make pre- and post-ASF comparisons by repeating the same wildlife sampling approaches (transects and camera trapping) previously employed at the site from 2013 to 2019. We posited that a decline in live pig activity and a dramatic (e.g., >10-fold) increase in carcasses would provide evidence of ASF triggering a mass mortality event. On the contrary, a decline in live animals without carcasses would suggest pigs migrated out of the areas, possibly driven by food scarcity or hunting, the former previously observed at Pasoh from 2002 to 2006 during the period when agricultural fruit from nearby oil palm plantations became unavailable (Luskin et al., 2017). We also investigated the onset and timing of the ASF outbreak, whether pig mortality was synchronous, and the locations that pig seek for dying, as this can have a substantial effect on soil nutrients (Brodie & McIntyre, 2019).

Practitioner points

- Develop monitoring systems to track wild pig populations in affected areas.
- Implement measures to prevent the spread of African swine fever (ASF) among wild pig populations, such as enhancing biosecurity measures in areas with known outbreaks and conducting widespread surveillance to detect and control ASF in wild pig populations.
- Invest in research to understand the ecological consequences of losing wild pigs, including impacts on soils, invertebrates, vertebrates, plants, and ecosystem processes such as carbon sequestration.

METHODS

Study site

The Pasoh landscape in Peninsular Malaysia is one of the flagship sites for permanent ecological monitoring by the Smithsonian Institution (Davies et al., 2020). Pasoh is home to a 50-ha forest dynamics plot censused every 5 years since 1986 (Davies et al., 2020), weekly phenology monitoring since 2003 (Chen et al., 2018), annual wildlife surveys by the Terrestrial Ecology, Assessment and Monitoring including camera trap surveys since 2013 (Jansen et al., 2014), hunting assessments since 2014 (Rooduijn, 2015), and experiments that link dynamics of humans, wildlife and plants ongoing since 1996 (Ickes, 2001; Ickes et al., 2005; Luskin et al., 2021). The habitat is primary and selectively logged lowland rainforest with a canopy dominated by trees in the Dipterocarpaceae family. There is a diverse wildlife community with an elevated population of wild boars (*S. scrofa*) that consume nearby oil palm fruits (Luskin et al., 2017) but bearded pigs (*S. barbatus*) have been absent from the landscape for two decades (Ke & Luskin, 2019; Luskin & Ke, 2017).

The arrival of ASF and wild boar carcasses

The presence of ASF was established at the Pasoh Research Forest by the World Organisation for Animal Health (WOAH), formerly the Office International des Epizooties, which is the leading intergovernmental organization coordinating, supporting, and promoting animal disease control (WOAH, 2022). Our staff at the Forest Research Institute of Malaysia (FRIM) has been

on-site continuously conducting a tree census within the 50-ha permanent forest dynamics plot since February 2022 and we also monitored the presence of wild boars and carcasses from March–July 2022. We estimated the time since death for all carcasses based on decay rates that have been previously studied at our site (Chin et al., 2008, 2007). Wild boar carcass decomposition in Malaysia shows little bloating and minor smell in the first 24 h, bloating and minimal smell in Days 2–4, obvious flesh decay and a putrid stench from 4 to 12 days, leaving dry remains of skin and bone after just 12–16 days (Chin et al., 2008, 2007). From 16 to 30 days, carcasses can still be identified by the lingering stench, enormous numbers of flies and larvae on the soil, and distinctive bones and skulls. Furthermore, we had high confidence in our ability to accurately identify the smell of wild boar carcasses because one succumbed under a field station structure. The smell of a rotting carcass was detectable within a 10–20 m radius. We considered carcass smells independent detections when they were >50 m apart, otherwise would do a search off-transect to locate them and be sure.

Transects

We conducted 1135 km of pre-ASF transects from 2014 to 2021. We took GPS fixes of all signs of hunting (snares, gun shells, traps), live animals, carcasses, and other notable observations of wildlife activity. After learning that ASF was confirmed at the landscape (WOAH, 2022), we mobilized the wildlife team to repeat the prior sampling approaches. We conducted 56 km of transects in June 2022 during our post-ASF fieldwork.

Camera trapping

We conducted systematic camera trapping annually from 2013 to 2018 (pre-ASF) and again in 2022 (post-ASF). Camera trapping grids ranged from 122 to 134 km^2 (minimum convex polygon around cameras). Each survey deployed 39-173 passive infrared camera traps (Bushnell or Reconyx brands) and used standardized methods, placing them along natural wildlife trails or angled towards small clearings and without baits, and attaching cameras to trees 0.2–0.3 m (Jansen et al., 2014). Cameras were deployed for approximately 30 days in 2013–2016, and in 2018, they were deployed year-round in 2017, and the post-ASF survey was 58 days in June–August 2022 (Z. Amir, Moore, et al., 2022; Dehaudt et al., 2022; Dunn et al., 2022; Hendry et al., 2023). We considered captures independent if they occurred at least 30 min apart.

RESULTS

The arrival of ASF and wild boar carcasses

Mortality of a forest-dwelling wild boar from ASF was confirmed at the Pasoh Research Forest on 10 February 2022 using PCR testing (details provided in WOAH outbreak reference: MVZT (PHG) 250/2022 "KG. SEBERANG JELAM", https://wahis.woah.org/#/in-review/4158; lat: 3.21702, long: 102.2664). During February, March, and April of 2022, there were occasional unusual observations of rotting wild boar carcasses and the associated stench. By May 9, we observed a wild boar mass mortality event in full swing, repeatedly encountering carcasses and the stench of rotting carcasses when entering the forest. The peak frequency of encountering carcasses occurred from May 15 to June 7 and then declined and became rare by July 15, 2022.

Carcass transects

During 56 km of intensive dedicated ASF transects surveyed from June 5 to 10, 2022, we observed 20 carcasses. Compared to the pre-ASF period (2014–2021) when only two carcasses were observed during 1135 km of transects, the number of wild boar carcasses post-ASF increased >100-fold (Table 1). There were 163 additional carcasses lying off the transects that were identified by smell only (Figure 1).

Of the 20 carcasses visually observed, three showed minimal bloating but a stench (2–4 days since death), three carcasses were in the advanced decomposition stage (4–12 days since death), and 14 carcasses were already dry but still retained a stench (12–30 days since death).

The 20 carcasses were found in a variety of locations, including 5 carcasses on trails or open areas, 5 carcasses adjacent to wild boar birthing nests, and 4 carcasses within wild boar birthing nests (Figure 2). Six carcasses were found in semi-secluded areas such as tree buttresses and under fallen trees. Two pairs of wild boars died next to each other. We observed no evidence of predation, scavenging, or other vertebrate disturbances to carcasses during transects.

TABLE 1 Signs of wild boars (*Sus scrofa*) and hunting in forests of the Pasoh landscape in Peninsular Malaysia from 2014 to 2022.

Year	Transects (km length)	Rotting carcasses (smell) per 100 km	Carcasses (visual) per 100 km	Hunting (snares, etc) per 100 km
2014	240	0	0.80	37.0
2015	225	0	0	0
2016	230	0	0	0
2017	180	0	0	0
2018	160	0	0	0.61
2019	100	0	0	0
2022	56	91.1	35.7	5.2

Note: Locations of any notable wildlife or hunting observations were collated in GPS tracks from >1000 km of transects hiked primarily to set camera traps. The dramatically increased mortality in May–June of 2022 coincides with the confirmed arrival of African swine fever in the area.

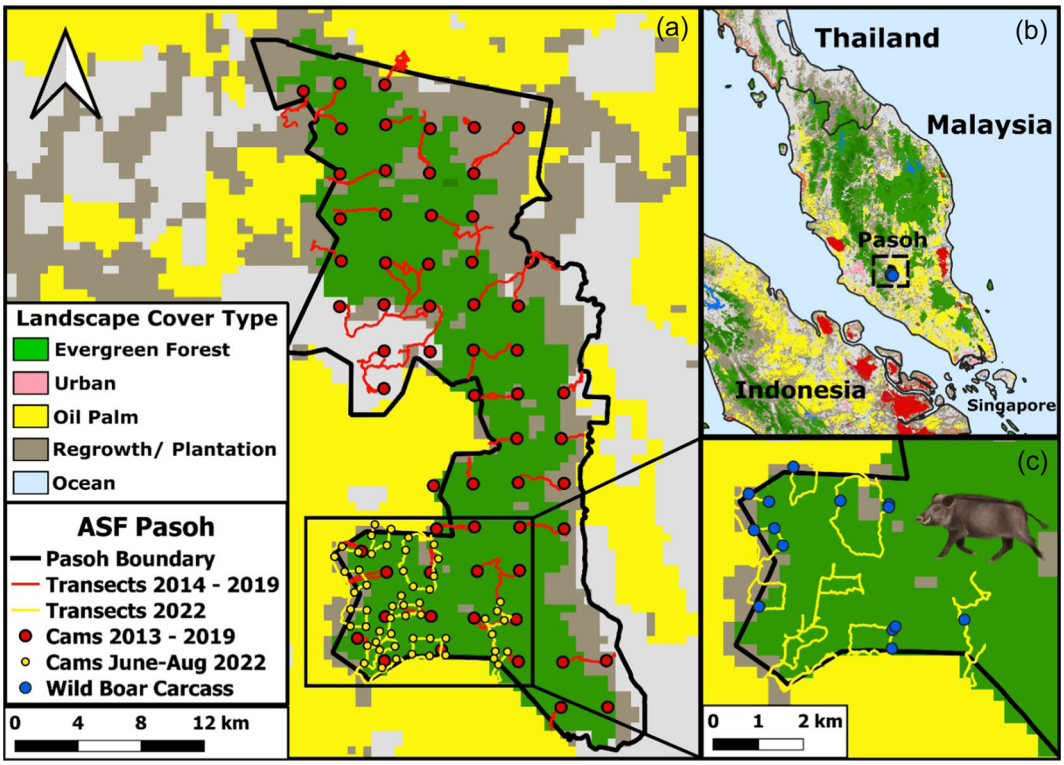

FIGURE 1 Transects walked and cameras set in the Pasoh landscape pre-ASF in 2014–2019 (panel a, red lines and points) in Peninsular Malaysia (panel b) and transects repeated in June 2022 during the initial onslaught of ASF (panel c, yellow lines; wild boar carcasses are shown with blue points).

FIGURE 2 Images of the wild boar mass mortality event triggered by ASF in Peninsular Malaysia. Panels (a) and (c) show carcasses within three days of death, panel (d) shows a decomposing carcass after 9–12 days, and panels (b) and (e) show "funeral nests" where dying animals sought shelter in abandoned wild boar birthing nests. All photos from the authors in early June 2022.

Wild boar activity in camera trapping

Camera trap observations of wild boar activity at the site revealed an 87% decline in capture rates in 2022 compared to average levels from five prior surveys spanning 2013–2017 (Figure 3). Specifically, the relative activity index or "RAI" (independent captures per 100 trap nights) averaged 25.56 from 2013 to 2017 and was

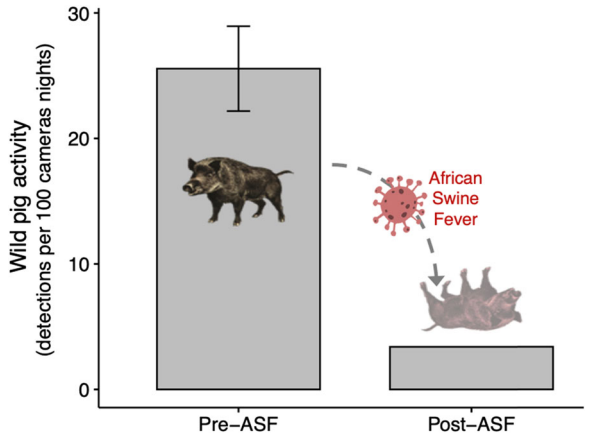

FIGURE 3 Activity levels of native wild boars (*Sus scrofa*) at the Pasoh landscape before ASF (2013–2019, "pre-ASF") compared to during the initial ASF onslaught in 2022 (post-ASF). The units for the relative activity index are independent captures per 100 trap nights.

TABLE 2 Wild boars (*Sus scrofa*) capture rates in camera trapping at the Pasoh landscape in Peninsular Malaysia from 2013 to 2022.

Year	Cameras	Trap nights	RAI
2013	58	1740	30.63
2014	57	1710	26.67
2015	59	1770	38.08
2016	42	2794	23.94
2017	173	10,534	19.36
2018	45	1661	14.69
2022	39	2268	3.40

Note: The units for the relative activity index (RAI) are independent captures per 100 trap nights.

just 3.39 in 2022 (Table 2). The only scavenging activity observed on cameras was a sun bear (*Helarctos malayanus*) eating maggots from a carcass during its advanced decomposition stage (4–12 days since death).

DISCUSSION

We observed a ~100-fold increase in wild boar (*S. scrofa*) mortality in June 2022 compared to prior years that coincided with the initial onslaught of ASF in Peninsular Malaysia. After a few cases in February, the virus appears to have been widely transmitted in April 2022. Following a 1- to 3-week incubation period (Liu et al., 2021), most mortality occurred within a 3-week period from mid-May to early June, which was corroborated by both the onsite FRIM staff and verified by the decomposition states of carcasses observed in early June. Live wild boar activity measured with camera traps declined dramatically by 87% suggesting that ASF killed the majority of the wild boars previously living at the site.

Wild boars sought existing birthing nests as locations to die ("funeral nests"), which is the first known observation of this behavior to our knowledge. The use of funeral nests may be perceived as safe places during vulnerable periods, similar to their motivation during birthing. We could not determine the sex of animals using funeral nests, but it is possible that the same sows that built nests for birthing also used them to die. We note that nests (dated by the decomposition of the vegetation) were much older than the carcasses within, reflecting the repurposing of existing birthing nests rather than the building of new nests. Wild boar carcasses appear to be in advanced decay within 2–3 weeks suggesting detecting ASF outbreaks requires timely surveillance in rainforest conditions and may have been missed in other locations, and that the carcass meat resource subsidy provided to predators and scavengers is extremely ephemeral.

RESEARCH IMPLICATIONS

Mass mortality events in multiple endemic wild pig species in Asia are likely driving a dramatic reorganization of forest ecology and present a unique opportunity for research. Changes in Malaysia's wild boar populations have been shown to drive understory vegetation dynamics with immense ecological repercussions (Ickes et al., 2005; Luskin et al., 2021) and more broadly in Southeast Asia (Bennett, 2000; Curran & Webb, 2000; Williams et al., 2021). For example, decades of high wild boar densities at Pasoh resulted in a 62% decline in tree sapling densities and an 86% increase in the liana saplings (Luskin et al., 2019). Work from other regions suggests that densities of saplings and small stems may rebound in the absence of wild pigs rooting and nest building, including bearded pigs in Borneo (Harrison et al., 2013). As pigs are generally seed predators (as opposed to dispersers), we also expect a pulse of seedling recruitment in the coming year(s), especially following the general flowering and mast fruiting events that characterize the forest phenology in much of Southeast Asia (Chen et al., 2018; Williams et al., 2021). At Pasoh and other landscapes with a prior hyperabundance of pigs, an important issue post-ASF is whether the trajectory of vegetation that was severely impacted by pigs makes a recovery, and if so, whether recovery resembles conditions before pig hyperabundance or moves to some novel state. We, therefore, urge ecologists to capitalize on this natural experiment and funding organizations to facilitate expedited support.

Our project also highlights the value of long-term monitoring for unexpected purposes. For example, our pre-ASF wildlife sampling was associated with questions about plant-animal interactions over longer ecologically meaningful timescales (e.g., Luskin et al., 2021) but also enabled this opportunistic study of a rare but important event. There are similar opportunities at other permanent forest plots in the region and globally (Davies et al., 2020).

CONSERVATION IMPLICATIONS

The sudden die-off of Asian wild pigs impacts other animal populations, including competitors and predators. Most terrestrial species in Asia directly or indirectly compete with generalist wild pigs for food.

This means that a sudden loss of wild pigs could benefit frugivores and granivores by providing access to additional fruiting materials, and benefit browsers such as ungulates (e.g., muntjac deer, *Muntiacus muntjac*) through the regrowth of the understory tree saplings. Wild pig rooting causes severe soil disturbances so their decline may benefit fossorial animals. As their prey base is depleted, carnivores such as tigers, leopards, and clouded leopards will likely switch to smaller, less energetically profitable prey, widening their diet breadths and reducing fitness (Z. Amir, Sovie, et al., 2022; Steinmetz et al., 2021).

The cascading impacts of declining wild pigs in Southeast Asia will also affect human economies and livelihoods (Luskin et al., 2020). Wild pigs are important species for some Indigenous cultures in Southeast Asia, especially in Borneo (*S. barbatus*) and New Guinea (*S. scrofa*, naturalized) where they play a central role in ancient hunting traditions, modern economies, and customary gift-giving and dowries (Bennett, 2000; Kurz et al., 2023, 2021; Luskin et al., 2014; Pattiselanno et al., 2020; Wiles, 2017; World Bank, 2021). As ASF eliminates options for sustainable pig hunting and husbandry, compensatory hunting targeting more endangered, rarer, and slower-reproducing wildlife may spell a conservation disaster. The loss in nutritional and cultural terms is likely to acutely impact the region's Indigenous peoples.

AUTHOR CONTRIBUTIONS

Matthew Scott Luskin: Conceptualization (lead); investigation (lead); project administration (lead); resources (lead); writing—original draft (lead); writing—review and editing (lead). **Jonathan H. Moore**: Conceptualization (equal); data curation (equal); investigation (equal); writing—review and editing (supporting). **Calebe P. Mendes**: Investigation (equal); writing—review and editing (equal). **Musalmah Bt Nasardin**: Project administration (supporting); writing—review and editing (supporting). **Monubu Onuma**: Conceptualization (supporting); project administration (supporting); writing—review and editing (supporting). **Stuart J. Davies**: Conceptualization (supporting); resources (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data is included within the actual paper.

ETHICS STATEMENT

This observational study did not require animal research ethics approval.

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REFERENCES

Amir, Z., Moore, J.H., Negret, P.J. & Luskin, M.S. (2022) Megafauna extinctions produce idiosyncratic Anthropocene assemblages. *Science Advances*, 8, eabq2307.

Amir, Z., Sovie, A. & Luskin, M.S. (2022) Inferring predator-prey interactions from camera traps: a Bayesian co-abundance modeling approach. *Ecology and Evolution*, 12(12). https://doi.org/10.1002/ece3.9627

Bennett, E.L. (2000) Saving Borneo's bacon: the sustainability of hunting in Sarawak and Sabah. In: Robinson, J.G. & Bennett, E.L. (Eds.) *Hunting for sustainability in tropical forests*. New York: Columbia University Press, pp. 305–324.

Brodie, J.F. & McIntyre, P.B. (2019) Bushmeat biogeochemistry: hunting tropical mammals alters ecosystem phosphorus budgets. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20190966.

Chen, Y.-Y., Satake, A., Sun, I.-F., Kosugi, Y., Tani, M., Numata, S. et al. (2018) Species-specific flowering cues among general flowering Shorea species at the Pasoh Research Forest, Malaysia. *Journal of Ecology*, 106, 586–598.

Chenais, E., Depner, K., Guberti, V., Dietze, K., Viltrop, A. & Ståhl, K. (2019) Epidemiological considerations on African swine fever in Europe 2014–2018. *Porcine Health Management*, 5, 6.

Chin, H.C., Marwi, M.A., Salleh, A.F.M., Jeffery, J., Kurahashi, H. & Omar, B. (2008) Study of insect succession and rate of decomposition on a partially burned pig carcass in an oil palm plantation in Malaysia. *Tropical Biomedicine*, 25, 202–208.

Chin, H.C., Marwi, M.A., Salleh, A.F.M., Jeffery, J. & Omar, B. (2007) A preliminary study of insect succession on a pig carcass in a palm oil plantation in Malaysia. *Tropical Biomedicine*, 24, 23–27.

Curran, L.M. & Webb, C.O. (2000) Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs*, 70, 129–148.

Davies, S.J., Abiem, I., Abu Salim, K., Aguilar, S., Allen, D., Alonso, A. et al. (2021) ForestGEO: understanding forest diversity and dynamics through a global observatory network. *Biological Conservation*, 253, 108907.

Dehaudt, B., Amir, Z., Decoeur, H., Gibson, L., Mendes, C., Moore, J.H. et al. (2022) Common palm civets *Paradoxurus hermaphroditus* are positively associated with humans and forest degradation with implications for seed dispersal and zoonotic diseases. *Journal of Animal Ecology*, 91, 794–804.

Denstedt, E., Porco, A., Hwang, J., Nga, N.T.T., Ngoc, P.T.B., Chea, S. et al. (2021) Detection of African swine fever virus in free-ranging wild boar in Southeast Asia. *Transboundary and Emerging Diseases*, 68, 2669–2675.

Dunn, A., Amir, Z., Decoeur, H., Dehaudt, B., Nursamsi, I., Mendes, C. et al. (2022) The ecology of the banded civet (*Hemigalus derbyanus*) in Southeast Asia with implications for mesopredator release, zoonotic diseases, and conservation. *Ecology and Evolution*, 12, e8852.

Ewers, R.M., Nathan, S.K.S.S. & Lee, P.A.K. (2021) African swine fever ravaging Borneo's wild pigs. *Nature*, 593, 37.

FAO. (2021) ASF situation update—African Swine Fever (ASF)—FAO Emergency Prevention System for Animal Health (EMPRES-AH). Available from: http://www.fao.org/ag/againfo/programmes/en/empres/ASF/situation_update.html

FAO, IUCN, & OIE. (2021) Conservation impacts of African swine fever in the Asia-Pacific region. Joint communique of the Food and Agriculture Organization of the United Nations (FAO),

International Union for Conservation of Nature Species Survival Commission (IUCN SSC) and the World Organisation for Animal Health (OIE). Bangkok, Thailand.
Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T. et al. (2013) Consequences of defaunation for a tropical tree community. *Ecology Letters*, 16, 687–694.
Hendry, A., Amir, Z., Decoeur, H., Mendes, C.P., Moore, J.H., Sovie, A. et al. (2023) Marbled cats in Southeast Asia: are diurnal and semi-arboreal felids at greater risk from human disturbances? *Ecosphere*, 14, e4338.
Ickes, K. (2001) Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland dipterocarp rain forest of Peninsular Malaysia. *Biotropica*, 33, 682–690.
Ickes, K., Paciorek, C.J. & Thomas, S.C. (2005) Impacts of nest construction by native pigs (*Sus scrofa*) on lowland Malaysian rain forest saplings. *Ecology*, 86, 1540–1547.
Jansen, P.A., Ahumada, J., Fegraus, E. & O'Brien, T. (2014) TEAM: a standardised camera trap survey to monitor terrestrial vertebrate communities in tropical forests. In: Meek, P.D. & Fleming, P.J.S. (Eds.) *Camera trapping: wildlife management and research*. Melbourne, Australia: CSIRO Publishing, pp. 263–270.
Ke, A. & Luskin, M.S. (2019) Integrating disparate occurrence reports to map data-poor species ranges and occupancy: a case study of the vulnerable bearded pig *Sus barbatus*. *Oryx*, 53, 377–387.
Khalidah, K.N., Wahdaniyah, S., Kamarudin, N., Lechner, A.M. & Azhar, B. (2021) Spared from poaching and natural predation, wild boars are likely to play the role of dominant forest species in Peninsular Malaysia. *Forest Ecology and Management*, 496, 119458.
Kurz, D.J., Connor, T., Brodie, J.F., Baking, E.L., Szeto, S.H., Hearn, A.J. et al. (2023) Socio-ecological factors shape the distribution of a cultural keystone species in Malaysian Borneo. *npj Biodiversity*, 2, 4.
Kurz, D.J., Saikim, F.H., Justine, V.T., Bloem, J., Libassi, M., Luskin, M.S. et al. (2021) Transformation and endurance of Indigenous hunting: Kadazandusun-Murut bearded pig hunting practices amidst oil palm expansion and urbanization in Sabah, Malaysia. *People and Nature*, 3, 1078–1092.
Lamperty, T., Chiok, W.X., Khoo, M.D.Y., Amir, Z., Baker, N., Chua, M.A.H. et al. (2023) Rewilding in Southeast Asia: Singapore as a case study. *Conservation Science and Practice*, 5, e12899.
Liu, Y., Zhang, X., Qi, W., Yang, Y., Liu, Z., An, T. et al. (2021) Prevention and control strategies of African swine fever and progress on pig farm repopulation in China. *Viruses*, 13, 2552.
Luskin, M.S., Brashares, J.S., Ickes, K., Sun, I.-F., Fletcher, C., Wright, S.J. et al. (2017) Cross-boundary subsidy cascades from oil palm degrade distant tropical forests. *Nature Communications*, 8, 2231.
Luskin, M.S., Christina, E.D., Kelley, L.C. & Potts, M.D. (2014) Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. *Human Ecology*, 42, 35–45.
Luskin, M.S., Ickes, K., Yao, T.L. & Davies, S.J. (2019) Wildlife differentially affect tree and liana regeneration in a tropical forest: an 18-year study of experimental terrestrial defaunation versus artificially abundant herbivores. *Journal of Applied Ecology*, 56, 1379–1388.
Luskin, M.S., Johnson, D.J., Ickes, K., Yao, T.L. & Davies, S.J. (2021) Wildlife disturbances as a source of conspecific negative density-dependent mortality in tropical trees. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20210001.
Luskin, M.S. & Ke, A. (2017) Bearded pig *Sus barbatus* (Müller, 1838). In: Melletti, M. & Meijaard, E. (Eds.) *Ecology, conservation and management of wild pigs and peccaries*. Cambridge, UK: Cambridge University Press, pp. 175–183.
Luskin, M.S., Meijaard, E., Surya, S., Walzer, C. & Linkie, M. (2020) African swine fever threatens Southeast Asia's 11 endemic wild pig species. *Conservation Letters*, 14, e12784.
Moore, J.H., Sittimongkol, S., Campos-Arceiz, A., Sumpah, T. & Eichhorn, M.P. (2016) Fruit gardens enhance mammal diversity and biomass in a Southeast Asian rainforest. *Biological Conservation*, 194, 132–138.
Oberin, M., Hillman, A., Ward, M.P., Holley, C., Firestone, S. & Cowled, B. (2022) The potential role of wild suids in African swine fever spread in Asia and the Pacific region. *Viruses*, 15, 61.
Pattiselanno, F., Lloyd, J.K.F., Sayer, J., Boedhihartono, A.K. & Arobaya, A.Y.S. (2020) Wild meat trade chain on the Bird's Head Peninsula of West Papua Province, Indonesia. *Journal of Ethnobiology*, 40, 202–217.
Rooduijn, B. (2015) Quantifying hunting effort and its impact on the terrestrial mammal community of Pasoh Forest Reserve, Malaysia. Thesis for the Wageningen University.
Steinmetz, R., Seuaturien, N., Intanajitjuy, P., Inrueang, P. & Prempree, K. (2021) The effects of prey depletion on dietary niches of sympatric apex predators in Southeast Asia. *Integrative Zoology*, 16, 19–32.
Weaver, T.R.D. & Habib, N. (2020) *Evaluating losses associated with African swine fever in the People's Republic of China and neighboring countries*. Mandaluyong, Philippines: Asian Development Bank.
Wiles, S. (2017) It's a pig's life in Papua New Guinea. MDF Exposure. Available from: https://mdf.exposure.co/its-a-pigs-life-in-papua-new-guinea
Williams, P.J., Ong, R.C., Brodie, J.F. & Luskin, M.S. (2021) Fungi and insects compensate for lost vertebrate seed predation in an experimentally defaunated tropical forest. *Nature Communications*, 12, 1650.
WOAH. (2022) African Swine Fever—case reference MVZT (PHG) 250/2022. Paris, France: World Organisation for Animal Health. Available from: https://wahis.woah.org/#/report-info?reportId=52902
World Bank. (2021) Rural population (% of total population)—Papua New Guinea Data. Available from: https://data.worldbank.org/indicator/SP.RUR.TOTL.ZS?locations=PG

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