The rise of hyperabundant native generalists threatens both humans and nature

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ABSTRACT

In many disturbed terrestrial landscapes, a subset of native generalist vertebrates thrives. The population trends of these disturbance-tolerant species may be driven by multiple factors, including habitat preferences, foraging opportunities (including crop raiding or human refuse), lower mortality when their predators are persecuted (the 'human shield' effect) and reduced competition due to declines of disturbance-sensitive species. A pronounced elevation in the abundance of disturbance-tolerant wildlife can drive numerous cascading impacts on food webs, biodiversity, vegetation structure and people in coupled human–natural systems. There is also concern for increased risk of zoonotic disease transfer to humans and domestic animals from wildlife species with high pathogen loads as their abundance and proximity to humans increases. Here we use field data from 58 landscapes to document a supra-regional phenomenon of the hyper-abundance and community dominance of Southeast Asian wild pigs and macaques. These two groups were chosen as prime candidates capable of reaching hyperabundance as they are edge adapted, with gregarious social structure, omnivorous diets, rapid reproduction and high tolerance to human proximity. Compared to intact interior forests, population densities in degraded forests were 148% and 87% higher for wild boar and macaques, respectively. In landscapes with >60% oil palm coverage, wild boar and pig-tailed macaque estimated abundances were 337% and 447% higher than landscapes with <1% oil palm coverage, respectively, suggesting marked demographic benefits accrued by crop raiding on calorie-rich food subsidies. There was extreme community dominance in forest landscapes with >20% oil palm cover where two pig and two macaque species accounted for >80% of independent camera trap detections, leaving <20% for the other 85 mammal species >1 kg considered. Establishing the population trends of pigs and macaques is imperative since they are linked to cascading impacts on the fauna and flora of local forest ecosystems, disease and human health, and economics (i.e., crop losses). The severity of potential negative cascading effects may motivate control efforts to achieve ecosystem integrity, human health and conservation objectives. Our review concludes that the rise of native generalists can be mediated by specific types of degradation, which influences the ecology and conservation of natural areas, creating both positive and detrimental impacts on intact ecosystems and human society.

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Key words: abundance, camera trapping, edge effects, fragmentation, hunting, plant–animal interactions, trophic cascades, wildlife ecology.

CONTENTS

I. INTRODUCTION

(1) Disturbance-tolerant wildlife

There are numerous reasons why native wildlife thrives near humans and human-modified landscapes, including favourable habitat features, foraging opportunities or reduced predation and competition (Gaynor *et al.*, 2019; Filgueiras *et al.*, 2021). Native terrestrial mammals are sustained in a variety of human–natural systems, where they are part of food webs, contribute to ecosystem processes and in turn provide humans with ecosystem services (Apfelbeck *et al.*, 2020; Collins, Magle & Gallo, 2021). These positive impacts are balanced by deleterious effects if wildlife poses risks to humans and livestock, such as direct attacks, *via* zoonotic diseases, or damage to crops or other products (Luskin *et al.*, 2017*b*, 2021*b*; Gibb *et al.*, 2020). Human tolerance of wildlife also depends on conservation threat levels. For example, Critically Endangered pangolins (*Manis javanica*) are tolerated in Singapore despite elevated zoonotic disease risks (IUCN, 2019; Nursamsi *et al.*, 2023), while Least Concern civets and bats hosting viral pathogens, including Nipah, SARS and likely COVID-19, may not be tolerated (Yu *et al.*, 2018; Gibb *et al.*, 2020; Dehaudt *et al.*, 2022; Dunn *et al.*, 2022). The densities of human commensal wildlife also shape attitudes towards the species and the magnitude of their positive or negative impacts.

(2) Wildlife in degraded habitats

Over 70% of the world's remaining forests are within 1 km of an edge (Haddad *et al.*, 2015). The increasing proportion of edge habitat negatively affects forest specialists and increases access for hunters, who preferentially target large-bodied vertebrates (Peres, 2001; Benítez-López *et al.*, 2017). While many species respond negatively to forest edges, a subset of generalist species can thrive in these degraded areas, particularly those species that can exploit disturbed and human-modified habitats and resources (Gibson, 2011; Luskin *et al.*, 2017*b*). These 'winners' can even reach hyperabundance, greatly exceeding natural densities supported by undisturbed habitats and consequently produce negative impacts on other native fauna and flora (Filgueiras *et al.*, 2021).

II. WILDLIFE HYPERABUNDANCE

(1) Definition

We define hyperabundance in native mammals as at least a doubling of their long-term population density, compared with similar habitats, that is driven by non-natural, human-caused conditions. This definition takes into account the known variation in densities within species that span multiple ecosystems (e.g. grasslands *versus* deciduous forests) or when they are closely tied to predator–prey dynamics (Berryman, 1992). Species like rodents with *r*-selected life histories (prolific reproduction, high mortality, short-lived) may appear predisposed to hyperabundance since they can double their populations within a single year (Fryxell, Sinclair & Caughley, 2014), but we reserve the term hyperabundance for situations with persistently elevated densities across multiple years (e.g. Gibson *et al.*, 2013; Moore *et al.*, 2022).

(2) Drivers of hyperabundance

Wildlife hyperabundance in degraded landscapes can arise through several processes. Species traits associated with hyperabundance may include being habitat and dietary generalists that naturally thrive in ecotones and edges, or species with high fecundity whose populations can respond to changing resources or withstand hunting pressure (Terborgh & Estes, 2013; Filgueiras *et al.*, 2021). Hyperabundance is also found in species that leave natural areas to exploit anthropogenic food subsidies (i.e. crop raiding) and in species considered unpalatable due to food taboos or that are uninteresting for the pet and medicine trade (Oro *et al.*, 2013; Luskin *et al.*, 2014, 2017*b*).

(3) Hyperabundance globally

Examples of hyperabundance can be found in a variety of species and ecosystems, indicating this is a global phenomenon (Fig. 1). Hyperabundant native generalists are often associated with humans and cause severe ecological damage (Estes *et al.*, 2011; Luskin *et al.*, 2017*b*) and alter plant and animal diversity (Estes *et al.*, 2011; Terborgh & Estes, 2013; Dirzo *et al.*, 2014; Ivey *et al.*, 2019). Hyperabundant species may also be associated with human–wildlife conflict such as crop raiding (Luskin *et al.*, 2014; Taylor *et al.*, 2016), property damage (Barrios-Garcia & Ballari, 2012), and outbreaks of zoonotic diseases such as rabies and Lyme disease (Levi *et al.*, 2012; Gibb *et al.*, 2020). There is an especially urgent need for a large-scale synthesis to understand the patterns, drivers, and consequences of hyperabundant generalist species in regions suffering high rates of biodiversity loss, habitat degradation, and histories of zoonotic disease emergence, all of which may be aggravated by high human population densities.

(4) Hyperabundance in Southeast Asia

Hyperabundance in Southeast Asia is poorly understood (Amir *et al.*, 2022*a*). To date, clear results have only been reported for Malayan field rats (*Rattus tiomanicus*) on man-made islands (Moore *et al.*, 2022), wild boar (*Sus scrofa*) in one forest in Peninsular Malaysia (Ickes, 2001; Luskin *et al.*, 2017*b*), and sporadic reports suggesting high densities of long-tailed macaques (*Macaca fascicularis*) that require management in Peninsular Malaysia (Choong *et al.*, 2021). There are no clear regional trends for pigs and macaques and these taxa are actually presumed to be declining in most accounts (Luskin & Ke, 2017; Luskin *et al.*, 2018, 2021*b*, 2023; Keuling & Leus, 2019; Ke & Luskin, 2019; Ruppert *et al.*, 2022; Hansen *et al.*, 2023). In Southeast Asia, there are reports of wild boars and bearded pigs *Sus barbatus* benefiting from oil palm but these all arose from single-landscape studies. Studies at Pasoh Forest Reserve in Peninsular Malaysia (Ickes, Dewalt & Appanah, 2001; Luskin *et al.*, 2017*b*), Sumatra (Luskin *et al.*, 2014), and Sabah, Borneo (Love *et al.*, 2017) have shown positive responses of wild boars and bearded pigs to oil palm. There is equally as much work suggesting wild boars and bearded pigs are declining in the region (Harrison *et al.*, 2016; Luskin *et al.*, 2018) with the lethal onslaught of African Swine Fever threatening extirpations and extinctions (Luskin *et al.*, 2021*b*, 2023). For macaques, recent work suggested that pig-tailed macaques *Macaca nemestrina* are increasingly threatened, leading to the IUCN *Red List* upgrading their threat status from Vulnerable to Endangered, i.e. the opposite of hyperabundance (Ruppert *et al.*, 2022).

(5) Study species

We chose to focus on four pig and macaque species that have importance ecologically, culturally, and/or economically. These species are also the most frequently detected in camera trapping studies in Southeast Asia, together often accounting for >50% of detections: wild boar (*Sus scrofa*), bearded pig (*Sus barbatus*), pig-tailed macaque (*Macaca nemestrina*) and long-tailed macaque (*Macaca fascicularis*). These species possess several characteristics that make them prime candidates for
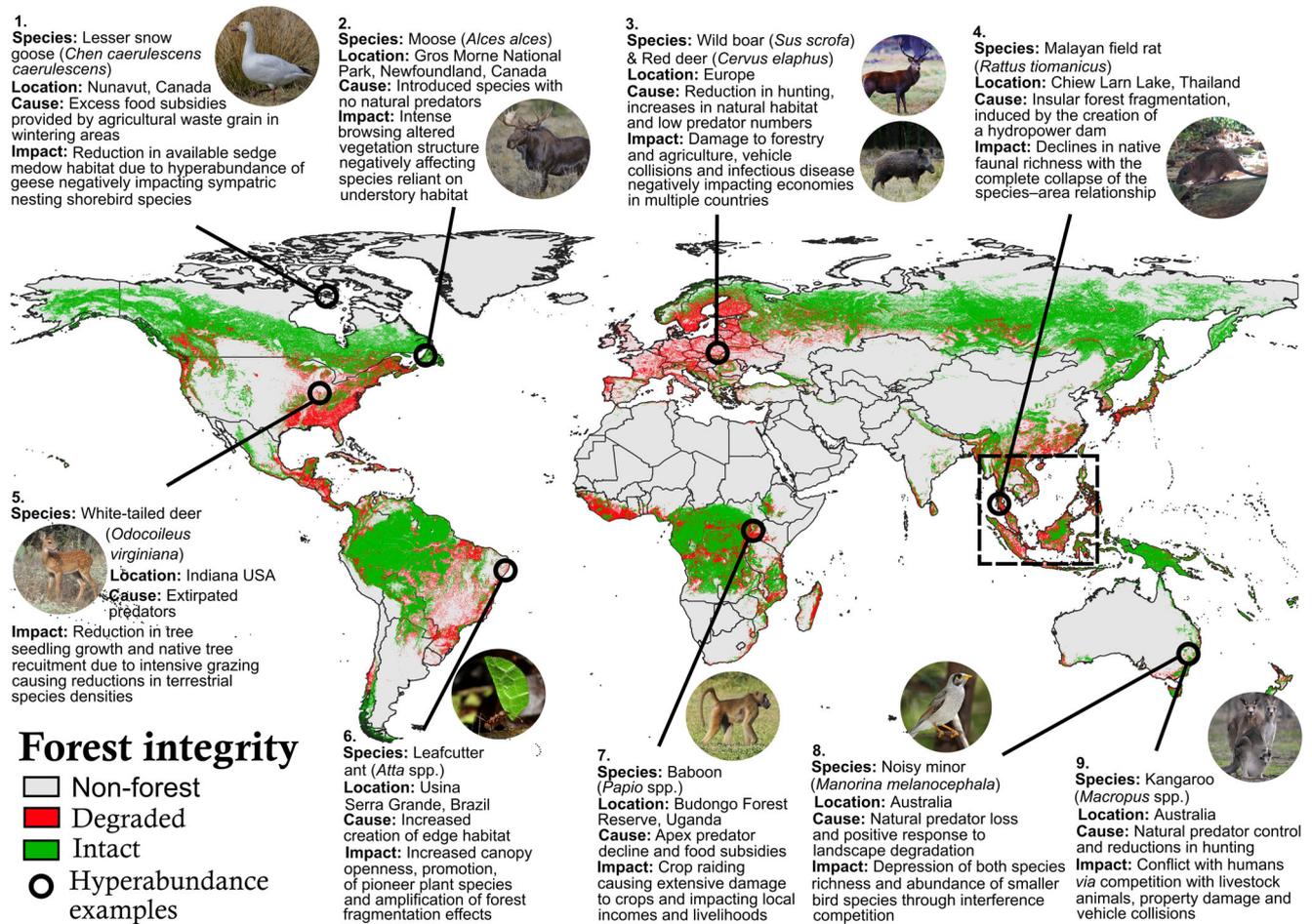
Fig. 1. Examples of hyperabundant native wildlife. The dashed square indicates our study area. Colours on the map represent the Forest Landscape Integrity Index (FLII), which incorporates forest size, distance to edge, degree of fragmentation, and logging, with a range of 0 (most disturbed) to 10 (most undisturbed). Degraded forest was defined as cells with FLII scores from 0 to <7 (red) and intact forest as scores from 7 to 10 (green) using data generated by Grantham *et al.* (2021). Oil palm is shown in purple. References for examples of hyperabundance: 1, Flemming *et al.* (2019); 2, Rae *et al.* (2014); 3, Valente *et al.* (2020); 4, Moore *et al.* (2022); 5, Shelton *et al.* (2014); 6, Meyer *et al.* (2009); 7, Taylor *et al.* (2016); 8, Melton *et al.* (2021); 9, Wilson & Edwards (2019).

reaching hyperabundance: they have generalist omnivorous diets, are found in disturbed forests, and exhibit rapid reproductive rates (Love *et al.*, 2017; Luskin & Ke, 2017; Ruppert *et al.*, 2018, 2022; Ke & Luskin, 2019; Hansen *et al.*, 2020; Luskin *et al.*, 2023). These traits could potentially allow their populations to respond rapidly to changes in food, predation, and competition, and all four species are gregarious and group living and thus may be able to achieve higher densities than territorial solitary animals.

Establishing the population trends of pigs and macaques is imperative since they are linked to cascading impacts on the fauna and flora of local forest ecosystems, and human health and economics (Bueno *et al.*, 2011; Gibson *et al.*, 2014; Luskin *et al.*, 2014, 2017b; Cuevas *et al.*, 2020). Pigs (*Sus* spp.) and macaques (*Macaca* spp.) host high pathogen loads and are known to carry several diseases, including brucellosis, leptospirosis, Nipah, tuberculosis and Japanese encephalitis (discussed further in Section V.5). These species also share high

rates of immune similarity with humans, with recent evidence of simian malaria outbreaks in Central Kalimantan, Indonesia (Lee *et al.*, 2011; Barrios-Garcia & Ballari, 2012; Setiadi *et al.*, 2016) acting as disease reservoirs and providing considerable potential for zoonotic disease transfer to humans (Plowright *et al.*, 2017; Shah *et al.*, 2018; Gibb *et al.*, 2020).

(6) Research questions and hypotheses

Here we investigate if abundance is related to environmental variables (e.g. elevation) or disturbance variables (e.g. edges, logging, oil palm). We hypothesise that (*i*) macaque abundance will be positively related to all types of habitat degradation since they are edge specialists and rarely hunted; (*ii*) wild boar abundance will be unrelated to degraded habitats since they are edge specialists and are hunted to variable extents throughout the region; (*iii*) bearded pigs will be

negatively related to all types of degraded habitats since they are not considered edge specialists but are found in fragmented and logged forests and are actively hunted in their core range in Borneo; and (*iv*) oil palm might be driving pig and macaque densities in nearby forests, as crop-raiding pigs have been argued to benefit from oil palm kernel food subsidies in three previous studies at the individual-landscape level and macaques are edge-specialist frugivores. For all relationships, we predict that macaques will show stronger associations to habitat measured at local scales ($\sim$1 km^2) and pigs at larger scales (20 km^2) because pigs are more vagrant and exhibit less site fidelity (Melletti & Meijaard, 2017). We also verify if habitat associations gleaned from camera trap detections are also present in independent studies estimating densities.

III. METHODS

(1) Approach

We used a multi-scale approach because these adaptable species may respond differentially to local and landscape-level factors and adjust their movements and home range sizes (Thornton, Branch & Sunquist, 2011; Hansen *et al.*, 2020). First, we collated published density estimates to determine the drivers and absolute magnitude of changes in pig and macaque densities. Second, we utilised published camera trapping records to examine whether pigs and macaques show community dominance in degraded forests and near oil palm plantations at the landscape scale (comparing landscapes). Finally, we utilised new camera trapping records to test whether pigs and macaques became hyperabundant in degraded forests near plantations at the local scale (within landscapes).

(2) Study area

Our study area was defined as mainland Southeast Asia, Sumatra and Borneo for all landscape-level and camera-level analysis (Fig. 2A), excluding Java, the Philippines and anything east of Wallace's line. This study area was selected to match areas that share relatively consistent natural habitat conditions with predominately evergreen tropical forests and include the native distributions of at least three of our four study species (see online supporting information, Fig. S1).

For our landscape-level analyses of published densities and relative abundances in camera trapping, the exact sampling locations were obtained from the methods sections of published studies, or, when unavailable, we extracted coordinates from the study map (see Table S1 for density estimates and Tables S2 and S3 for relative abundance). If positional accuracy was a concern, we contacted the original authors for these details. Most camera trapping deployments covered large areas (10–1000 km^2) and were not arranged in a perfect grid or circle. To account for the lack of precision in

identifying the exact sampling area centroids, we generated covariates describing the landscapes within a 20 km radius (1256 km^2) using Geographic Information System (GIS) zonal statistics in the spatial analysis software QGIS (see Table S4 for sources of covariates used in generating species abundance estimates; Fig. S2). For the local-scale analyses from camera-level capture histories, we extracted covariates describing the areas within a 1 km radius ($\sim$3.14 km^2) of each camera. This distance was chosen as intermediate between the average home range size estimates for wild boars and macaques and has been used for studies focused on either genus (José-Domínguez, Savini & Asensio, 2015; Rayan & Linkie, 2020).

(3) Extracting standardised covariates to describe study areas

We focused on two covariates in testing the underlying drivers of pig and macaque hyperabundance and/or community dominance (Table S4). We used the Forest Landscape Integrity Index (FLII) values with 300 m pixel resolution to assess the influence of habitat degradation (edges, fragmentation, and logging; Grantham *et al.*, 2021). The FLII (hereafter 'forest integrity') is a globally consistent landscape-level index that incorporates forest loss, logging, and edges, as well as inferred effects from fragmentation and the loss of connectivity and is scaled between values of 0 = most degraded to 10 = most intact. Next, we quantified the percentage cover of oil palm in our study landscapes using the CRISP 2015 land cover map of Southeast Asia (Miettinen, Shi & Liew, 2016). This GIS layer includes 18 landscape types (including oil palm) at 250-m resolution.

There are various benefits and errors when integrating spatial covariates from many studies into standardised and consistent GIS layers. In particular, there may be some inaccuracies when extracting covariates from older studies (pre-2010) using GIS layers created after 2015, especially for the dynamic landscapes of Southeast Asia. However, the GIS layers we used rely upon numerous remote-sensing images obtained over multiple years and are the most robust sources currently available. For example, a pre-2010 study in an intact forest landscape may have suffered extensive clearing and oil palm establishment since 2010, and thus our method may incorrectly describe these coordinates as degraded with oil palm, when in fact at the time it was intact forest. Given recent ongoing clearing outpacing any reforestation in the study region, the direction of this bias is almost always to overestimate disturbance-sensitive species' presence in degraded areas, which reduces our statistical power. As a result, we likely underestimate true effect sizes, thereby yielding results that should be considered conservative.

(4) Macaques and wild boar density estimates

We collated published densities of pigs and macaques using a *Web of Knowledge* search performed with the search terms including common and scientific names AND dens* AND
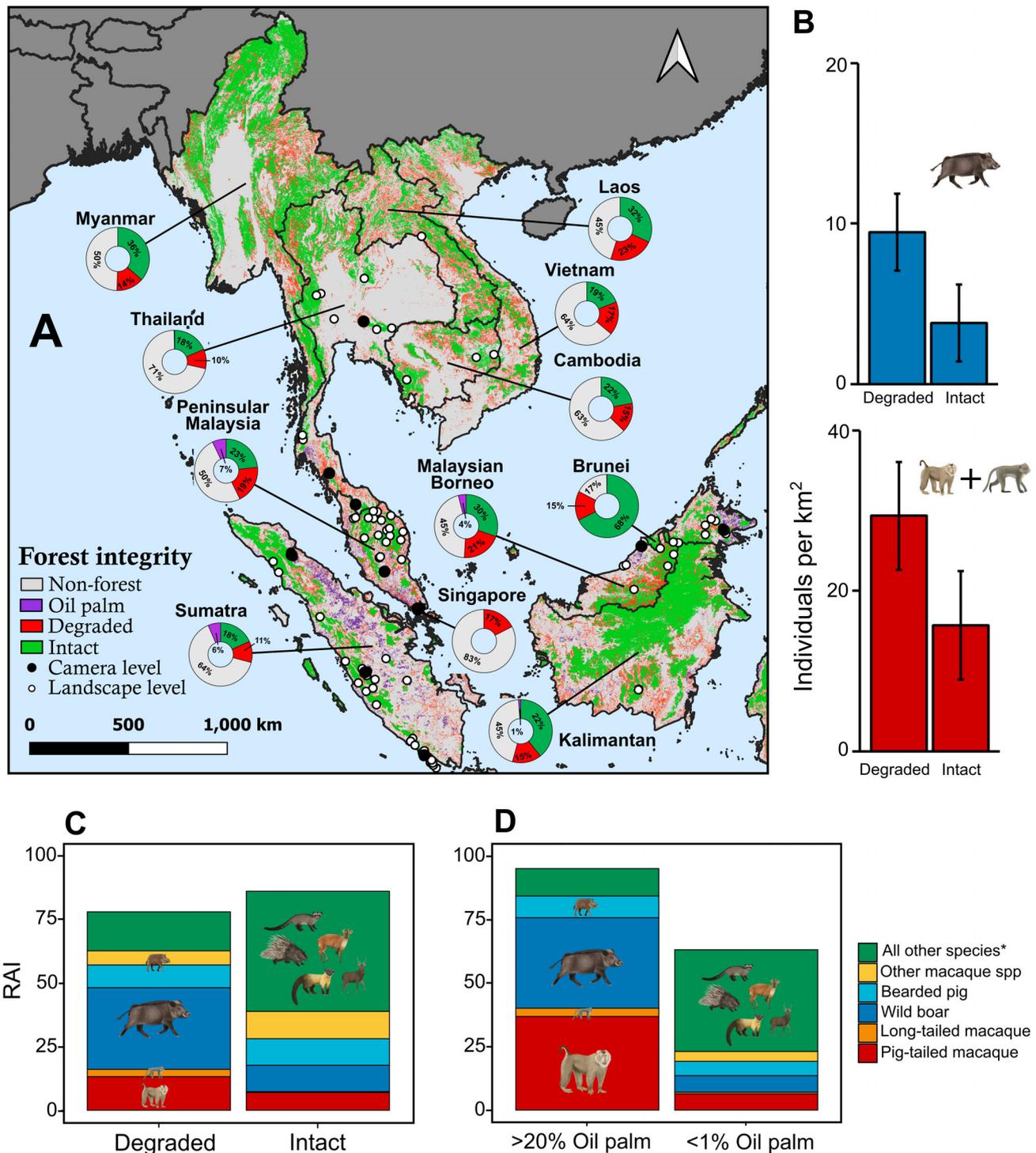
Fig. 2. Study region and study sites within Southeast Asia (A), pig and macaque densities (B) and relative abundance index (RAI; independent photographs per 100 trap nights) in camera trapping studies (C, D). We compared RAI between degraded [Forest Landscape Integrity Index (FLII) 0 to <7] and intact landscapes (FLII 7–10) (C) and between areas with high (>20%) and low (<1%) oil palm cover (D). In (A), the doughnut charts depict the percentage of each landscape classification per country. (B) provides the mean ± S.E.M for 44 and 19 published density estimates of wild boar (top) and long-tailed and pig-tailed macaques (bottom), respectively, across the study region. In (C) and (D), stacked bar charts show the average estimated RAI per species from 117 published camera trapping studies. *All other species includes 80 terrestrial vertebrates >1 kg. Statistical tests and box plots for (B–D) are presented in Figs S4–S6.

Asia. We also investigated citations within the identified papers for density estimates and included any suitable papers. This resulted in 23 density estimates for macaques (nine for pig-tailed macaques and 14 for long-tailed macaques), across 13 landscapes from 14 publications. We found a total of 79 density estimates for wild boar across 41 landscapes from 47 publications; there were no bearded pig density estimates so they were excluded from this analysis (Table S1). We estimated mean densities in intact and degraded forests using linear mixed-effects models (LMMs) with the R-package *lme4* (Bates *et al.*, 2015), with landscape included as a random effect to account for multiple observations from the same area. As there are relatively few density observations for macaques, we grouped pig-tailed and long-tailed macaques (same genus and with similar diets/behaviour) and included both species and landscape as random effects (Table S5). We feel it is appropriate to pool these two species in this analysis. We note that the original density estimates did not all employ standardised sampling or analytical methods and this could introduce additional noise.

(5) Pig and macaque abundance among landscapes

We examined the landscape-level predictors of pig and macaque abundance using capture rates from published camera trapping studies in Southeast Asia (Fig. 2C, D). We identified published camera trapping studies using a *Web of Knowledge* search performed with the criteria 'camera trap' AND any of our study countries, as well as Asia*, Malay*, Thai*, Sumatr* and Born*. We also performed the same search in *Google* to locate grey literature and academic theses. We retained studies that used unbaited camera deployments in forest, and which reported the full species capture lists (number of independent photographs of all mammals >1 kg) and the trapping effort (trap nights) (Tables S2 and S3). We refer to the area sampled as a 'landscape', which was usually a national park, production forest, or collection of nearby forest patches, and our final sample size was 164,055 detections of 89 species from 43 studies and 58 landscapes. We used 20-km radius buffers to extract landscape covariates providing average forest integrity values and landscape-scale percentage oil palm cover. We used published camera trap data to assess relationships between pig and macaque capture rates and landscape covariates (forest integrity and % oil palm cover). We used generalised linear mixed models (GLMMs) with the number of independent captures as the response variable (count data, assuming Poisson distribution), controlling for sampling effort as a model offset, and including 'landscape' as a random effect. Significance was assessed using the *z*-value and Satterthwaite approximations for degrees of freedom using *lmerTest* in R (Kuznetsova, Brockhoff & Christensen, 2017). Since we make comparisons within species and using similar sampling protocols, we assume that detectability does not vary systematically with our covariates, and therefore infer that differences in capture rates reflect true differences in abundance. We also used relative abundance index (RAI) from the

published camera trap data to run LMMs to assess community dominance of pigs and macaques. Our RAI comparisons were performed by separating forest integrity into two groups [high (values 7–10) and low forest integrity (0 to <7)] and separating oil palm landscapes into high (area > 20%) and low oil palm cover (area <1%), and we ran separate LMMs for all four pig and macaque species.

(6) Local pig and macaque abundance within landscapes

We conducted 20 new camera trapping sessions in 10 landscapes in Thailand (two sites), Peninsular Malaysia (two sites), Singapore (one site), Sumatra (three sites) and Borneo (two sites) to assess the effects of local habitat characteristics on relative abundances (see Table S6 and Appendix S1 for site description and trap deployment details). We produced detection history matrices using the total number of individuals detected within a sampling occasion of 3 days to reduce zero-inflation, and spatially resampled all cameras into hexagonal grid cells of equal size (0.86 km^2, hereafter 'sampling units') to satisfy spatial independence (Fig. S3; see Appendix S1 for detailed methods; Rayan & Linkie, 2016). Habitat covariates were averaged when there were multiple cameras within the same cell. We used hierarchical N-mixture (NM) models to estimate the relative abundance of pigs and macaques while accounting for imperfect detection using the *pcount()* function in *unmarked* in R (Royle, 2004; Fiske & Chandler, 2011). NM models provide an unbiased relative abundance metric (hereafter 'estimated abundance'), allowing for robust comparisons across multiple surveys for species that cannot be identified individually (Royle, 2004). We included 'landscape' as a fixed effect to account for three landscapes sampled over multiple trapping sessions and included sampling effort as a fixed effect on the detection probability formula to account for multiple cameras in the same grid cell (Table S7). We ran the same NM models for all species and tested if estimated abundance varied with forest integrity and percentage of oil palm plantations within 1 km of each camera.

IV. RESULTS ON HYPERABUNDANCE IN SOUTHEAST ASIA

(1) Densities

Population densities of wild boar were 148% higher (LMM: $t_{50.1} = -2.35$, $P = 0.023$) in degraded landscapes (mean $\pm$ S.E.M = 9.5 ± 1.9 individuals/km^2) compared with intact landscapes (3.8 ± 2.4 individuals/km^2) (Fig. 2B; see Fig. S4 for results of statistical tests). Macaques (both species combined) were 87% higher (LMM: $t_{15.2} = -2.03$, $P < 0.059$) in degraded landscapes (29.4 ± 5.9 individuals/km^2) compared with intact landscapes (15.7 ± 6.7 individuals/km^2) (Fig. 2B). Pig-tailed macaques, when considered separately, showed densities 69.7% higher in degraded

landscapes (24.1 ± 6.7) compared with intact landscapes (14.2 ± 0.7) (LMM: $t_2 = -13.33$, $P < 0.005$; Table S5). Long-tailed macaques could not be modelled separately due to insufficient data from intact forest sites for a statistical test but the mean density for degraded landscapes was 520% higher with 31 individuals/km^2 compared to 5 individuals/km^2 for intact forest.

(2) Community dominance

When comparing communities from intact *versus* degraded forest landscapes, the community dominance of pigs and macaques (i.e. the total RAI of the four focal species) rose from 32.7% to 73.2% of all independent captures, and when comparing low (<1%) to high (>20%) oil palm cover, the community dominance of pigs and macaques rose from 30.4% to 88.7% (Fig. 2C,D; see Tables S8 and S9 and Figs S5 and S6 for data from individual species). These shifts in community dominance were driven both by higher detection rates of the four generalist species and lower detection rates of forest specialists (Fig. 2C, D). In fact, pooled detections of the other 85 wildlife species >1 kg were 63.9% lower in degraded landscapes (LMM: $t_{65} = 2.95$, $P < 0.004$; Fig. 2C) and 75.5% lower in high (>20%) oil palm cover landscapes (LMM: $t_{56} = 2.88$, $P < 0.005$; Fig. 2D).

(3) Landscape-level determinants of hyperabundance

When examining habitat relationships using Poisson GLMMs with detections as a response variable and the continuous landscape-level predictors we found strong but not entirely consistent patterns. Long-tailed macaques showed a negative relationship with forest integrity (GLMM: $z = 5.81$, $P = 0.002$), while bearded pigs showed a significant positive relationship with forest integrity (GLMM: $z = 3.94$, $P = 0.008$). There were no significant relationships between forest degradation and wild boar or pig-tailed macaques (Fig. 3C). Relationships between the percentage oil palm in the landscape and wild boar and long-tailed macaque abundance were significantly positive (GLMM: $P < 0.01$ for both species) while no significant relationship was found for pig-tailed macaques or bearded pigs (Fig. 3D).

(4) Local determinants of hyperabundance

At the local scale, the estimated abundance from NM models was higher for three of the four species when sites with the minimum and maximum observed forest degradation were compared: wild boar = +196% 95% confidence interval (CI) = 195.6–197.3%), long-tailed macaque = +456.7% (95% CI = 437.4–476.7%) and pig-tailed macaque = 62.9% (95% CI = 62–63.9%; all NM: $z = <-5$, $P < 0.0001$) (Fig. 3A). However, abundance was 77.8% (95% CI = 76.3–79.3%) lower for bearded pigs at the most degraded sites ($z = 8.5$, $P < 0.0001$; Table S7). Estimated abundance was higher for all four species when comparing between landscapes with the

minimum (<1%) and maximum (>60%) observed oil palm cover [wild boar = +336.7% (95% CI = 306.5–369.3), bearded pig = +655.3% (95% CI = 571.1–750.1), long-tailed macaque = +9036.8% (95% CI = 8899.8–9175.9%), pig-tailed macaque = +447.3% (95% CI = 426.6–468.7; all NM: $z = >15$, $P < 0.0001$; Fig. 3B; Table S7].

V. THE CAUSES AND CONSEQUENCES OF HYPERABUNDANCE

(1) Pig and macaque hyperabundance

We document the hyperabundance of pigs and macaques across Southeast Asia. The *Sus* and *Macaca* genera now comprise the majority of all terrestrial vertebrates detected on camera traps in disturbed forests, constituting 73.2% and 88.7% of all captures in degraded forests and landscapes with >20% oil palm cover, respectively. These results show strong community dominance. Examples of hyperabundant native generalists can be found globally, including baboons in Africa, mesopredator release in North America and deer and pig species in Europe. Hyperabundance is often triggered by a reduction in top-down control by native predators, or by the presence of food subsidies, especially for disturbance-tolerant species and high-fecundity species (Rae, Whitaker & Warkentin, 2014; Luskin *et al.*, 2017*b*; Flemming *et al.*, 2019; Valente *et al.*, 2020).

Based on our definition of hyperabundance in mammals, describing the elevated numbers of Southeast Asia's pigs and macaques as hyperabundance is warranted for several reasons. First, our comparisons are limited to habitats that are predominantly tropical evergreen forests and include many observations from the same landscapes. Second, our study includes observations extending over more than 20 years, suggesting the observed trends are not ephemeral. Third, neither pigs nor macaques fit cleanly into either *r*- or *K*-selected life histories. Compared to similarly sized species, pigs are able to reproduce rapidly producing up to two large litters per year under ideal conditions with plentiful resources (Bywater *et al.*, 2010; Croft *et al.*, 2020) while also being comparatively long-lived (Fryxell *et al.*, 2014). Fourth, we identify *in situ* anthropogenic environmental drivers including habitat degradation and food subsidies from oil palm plantations as deviations from natural long-term conditions.

(2) Degraded forest and agricultural food subsidies

At the landscape scale, habitat associations with forest degradation were unclear for wild boar and pig-tailed macaques, whereas long-tailed macaques performed better in degraded landscapes and bearded pigs performed worse. High oil palm coverage (>20%) elevated the abundance of both wild boar and long-tailed macaques. Densities at the landscape scale were also higher in degraded habitats for both wild boar and macaques. At the local scale, which considered the 3.14 km^2 areas around cameras, habitat degradation and
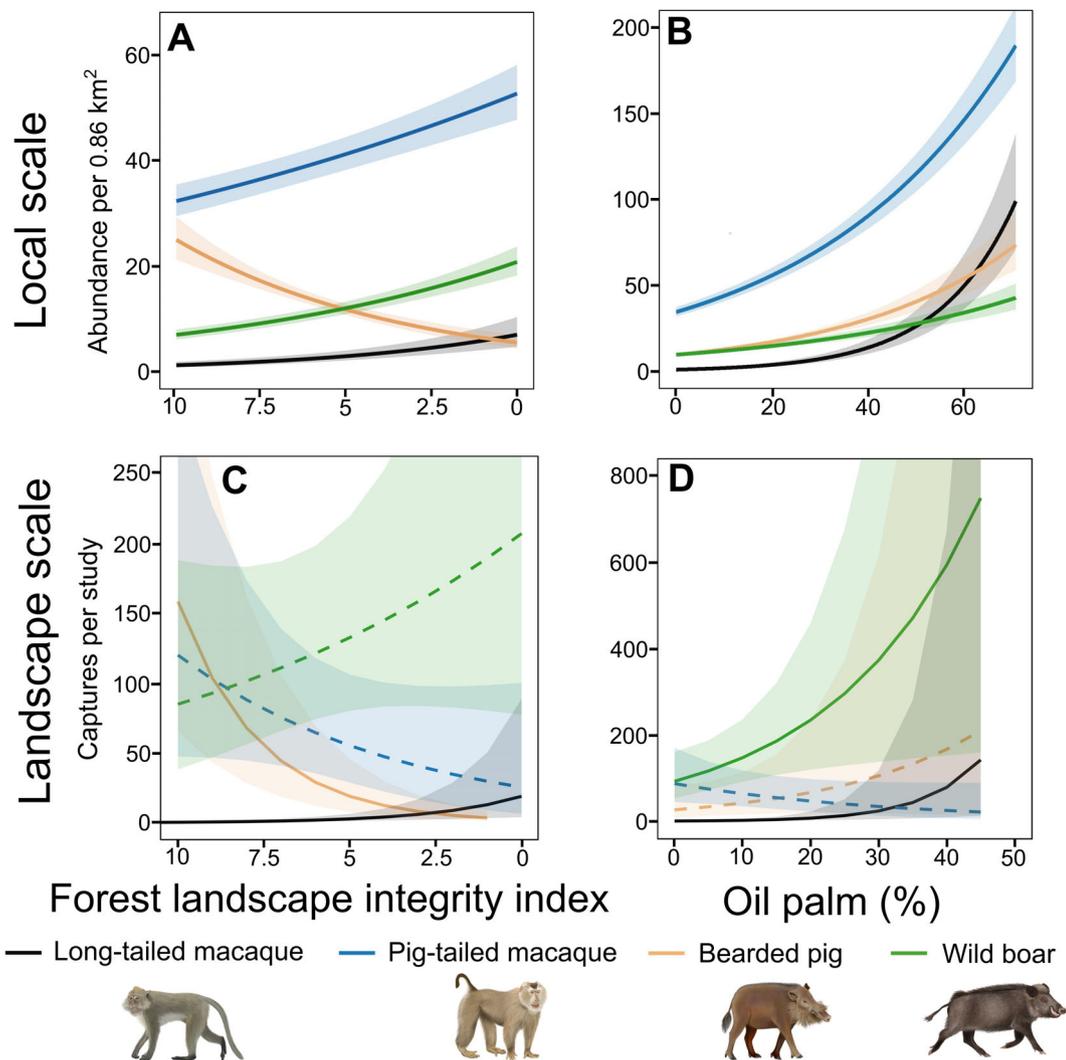
Fig. 3. Pig and macaque abundance in relation to forest integrity and oil palm agriculture in the landscape. The local-scale panels (A, B) show estimated abundance per 0.86 km^2 hexagonal grid cell across 10 newly sampled landscapes in Southeast Asia from N-mixture detection-corrected hierarchical modelling with covariates measured within 1 km of each camera. The landscape-scale panels (C, D) show estimated detections per study from generalised linear mixed models (GLMMs) with covariates averaged over 20 km radius study areas ($N = 117$ published data sets). Solid lines indicate a significant trend ($P < 0.05$), and shaded regions show 95% confidence intervals. Note forest integrity is descending so that intact landscapes are on the left and more degraded landscapes are on the right.

oil palm cover were consistently associated with elevated population abundance of wild boar and macaques. The positive association between bearded pigs and forest integrity, both within and across landscapes, may suggest a preference for primary forest adjacent to oil palm plantations. This is supported by a previous study in Borneo showing that bearded pigs utilise oil palm landscapes but prefer adjacent forested areas for a wider range of their behaviours (Love *et al.*, 2017). Taken together, our results likely reflect both that degraded areas have higher densities of pigs and macaques, and that mobile individuals (and groups) within these landscapes prefer edges near oil palm, as opposed to forested areas further from edges.

Our results documenting the highest pig and macaque densities near oil palm plantations align with other work in Malaysia showing abnormally high wildlife abundances within forest fruit gardens (Moore *et al.*, 2016). This suggests that supplementary food can release wildlife from natural bottom-up regulation imposed by resource scarcity, which may be especially important in Southeast Asian forests where the fruiting phenology of most canopy trees shows a supra-annual masting cycle (Curran & Leighton, 2000). Only certain habitat-generalist species can access food subsidies beyond forest edges, such as those provided by oil palm plantations, so there may be asymmetric competition with other herbivores. Habitat and dietary generalists such as pigs and

macaques that thrive in ecotones frequently raid cultivated crops, and consume both native plant material and human refuse from farmers living within oil palm landscapes (Bieber & Ruf, 2005; Barrios-Garcia & Ballari, 2012), likely out-competing deer, tapirs, and other vertebrate herbivores and omnivores in these degraded habitats.

(3) Other factors supporting hyperabundance

There are three other reasons for the success of pigs and macaques in degraded forest landscapes. First, both pigs and macaques have high fecundity, allowing them to exploit resources rapidly, tolerate hunting pressure, and recover quickly from disturbances. Second, large mammalian predators often avoid degraded habitats and oil palm, indirectly benefitting prey species capable of exploiting those same areas (Brodie, Giordano & Ambu, 2015; Luskin, Albert & Tobler, 2017a). Third, pigs and macaques are rarely targeted by hunters throughout regions where Islamic religious practices are observed, since the Halal diet forbids pork and fanged animals, including macaques (Luskin et al., 2014). The exception is areas in Borneo occupied by the Dayak people who often hunt bearded pigs (Luskin et al., 2014; Kurz et al., 2021, 2023).

(4) Consequences of wildlife hyperabundance for forests

Our findings have important conservation implications. Hyperabundant omnivorous ungulates and primates can alter vertebrate food webs through direct predation of smaller animals such as rodents, reptiles and birds (Ruppert, Mansor & Shahrul Anuar, 2014; Ruppert et al., 2018; Law, Ruppert & Holzner, 2018), disturb nesting sites (Mori et al., 2021), exert exploitative competition of a shared resource (Ilse & Hellgren, 1995; Barrios-Garcia & Ballari, 2012) and induce indirect effects through degradation of understory structure (Luskin et al., 2019, 2021a; Mori et al., 2021). Altered understory structure occurs through intense soil disturbance and direct seed/seedling predation (Bueno et al., 2011; Cuevas et al., 2020) and promotes the spread of invasive plant species (Fujinuma & Harrison, 2012), facilitates liana proliferation on host trees (Luskin et al., 2019), and alters tree diversity (Luskin et al., 2017b, 2021a). Further, pig soil disturbances in their invasive range are thought to impact carbon storage potential by driving greenhouse gas emissions representing up to 0.4% of annual land-use and forestry emissions (Terborgh & Estes, 2013; Dirzo et al., 2014; Chanthorn et al., 2019; O'Bryan et al., 2021), and there is little reason to suggest that their hyperabundance within native ranges would not produce similar levels of emissions. The sustained hyperabundance of pig and macaque populations in degraded forests and near oil palm plantations may deplete natural forest tree seeds during a mast, thus reducing seedling recruitment and future forest regeneration, and thereby undermining the strategy of predator satiation (Janzen, 1974; Curran & Leighton, 2000; Jia et al., 2018; Luskin et al., 2019, 2021a;

Williams et al., 2021). The influence of hyperabundant macaques on biotic communities is less well understood, but we note that their seed-dispersal capacity appears to be limited for large-seeded plant species (Nakashima & Sukor, 2010).

(5) Consequences of wildlife hyperabundance for humans

The hyperabundance of pigs and macaques also has important impacts on humans, since they drive economic damage from crop-raiding and display highly aggressive behaviour towards humans, even in urban settings (Priston & McLennan, 2013; Luskin et al., 2017b; Ilham et al., 2017; Balasubramaniam et al., 2020). Pigs are an amplifying host in which zoonotic viruses can modify for transmission to humans, whereas macaques can act as both reservoirs and amplifiers. The rise of pigs and macaques has been implicated in a higher potential for zoonotic disease transmission (Gibb et al., 2020). For instance, zoonotic diseases such as malaria Plasmodium knowlesi have a geographic range limited by their mosquito vectors and simian hosts (Moyes et al., 2014), but as landscapes become increasingly degraded zoonotic host populations both expand and also increase their proximity to humans, elevating disease risk. This is evident in Malaysian Borneo where human malaria outbreaks – mediated by macaques as zoonotic carriers (Fornace et al., 2016) – have increased. Cases of the zoonotic disease monkeypox have increased throughout 2022; this virus was first named and classified from samples taken from long-tailed macaques in Denmark in 1958 (Magnus et al., 2009; Liu et al., 2022). Nipah is spread by wild boars in Malaysia and Singapore (Yu et al., 2018), and tick-borne disease transfer from wild boars occurs in Europe (Hrazdilová et al., 2021; Castillo-Contreras et al., 2022). Both species also carry a variety of helminths (e.g. parasitic worms) that plague human health in developing countries. Domestic livestock are also threatened by disease transfer from pigs, including African swine fever and foot-and-mouth disease (Denstedt et al., 2021).

(6) Managing hyperabundant wildlife

Hyperabundant species can impact humans and local fauna and flora in a multitude of negative ways, requiring extensive control measures (Taylor et al., 2016; Wilson & Edwards, 2019; Moore et al., 2022). There are significant efforts to manage hyperabundant pig and macaque populations in Malaysia, Singapore and Indonesia (Luskin et al., 2014; Lamperty et al., 2023). Population control through cage trapping, culling, hunting and sterilisation may be effective when adequate resources are available (Priston & McLennan, 2013; Luskin et al., 2014; Croft et al., 2020). However, the high fecundity of these species makes control difficult as success (e.g. >50% population decline) would require high-intensity management for prolonged if not indefinite periods (Annapragada et al., 2021).

Management efforts to limit pig and macaque access to oil palm have largely failed. Luskin *et al.* (2017b) describe an attempt by the FELDA oil palm company to prevent wild boar from killing oil palm seedlings in Peninsular Malaysia. They constructed a 1 m trench with 1.5 m solid metal sheeting mounted vertically above the trench and stretching along approximately 5 km of the forest-plantation edge. Within weeks the trench had flooded, the pigs enjoyed these areas as pseudo-wallows, and then they dug underneath or pushed over the compromised fence. Macaque species can similarly negotiate fencing with ease (Mysterud & Rolandsen, 2019). Likewise, as semi-natural buffer zones between forests and plantations are also likely to be advantageous for pigs and macaques, such 'designer landscapes' are unlikely to improve the situation (Reidy, Campbell & Hewitt, 2008; Koh, Levang & Ghazoul, 2009). Another focus should be on limiting further oil palm expansion into surrounding intact forests, and instead exploiting already disturbed areas (Luskin & Potts, 2011). Long-term monitoring data focused on species abundance are essential to assessment of baseline population levels and of the effectiveness of ongoing management techniques. In the meantime, we recommend the prevention of future development of agriculture within close proximity to intact forests which could provide food subsidies to generalist species.

VI. KNOWLEDGE GAPS AND CAVEATS

(1) The roles of predators, competitors, and hunting

The role of hyperabundant native generalists in providing supplementary prey for carnivores has received little attention, nor has the role of hyperabundant native generalists on competitors, except for rodents on island fragments in Thailand (Moore *et al.*, 2022). Likewise, there is little known regarding the role of hunting in controlling pig and macaque populations, although this has been attempted for macaques in Peninsular Malaysia, and Dayak hunters in Sarawak nearly extirpated bearded pigs from a small forest adjacent to oil palm (Harrison *et al.*, 2016). Especially poignant in the region is the role of religion and culture in shaping hunting, wildlife abundance, and cascading impacts on forest ecology (Kurz *et al.*, 2021, 2023). Further research should also focus on the potential cascading impacts imposed by hyperabundant pigs and macaques in Southeast Asia, including their effects on vegetation structure, faunal communities, and human–wildlife conflicts. There is also an urgent need to improve disease monitoring of these species in this region, especially at edges where they are most likely to interact with domestic animals and humans. Further work on the top-down control of pigs and macaques is required to understand fully the mechanisms driving hyperabundance of generalist species in tropical forest regions (Amir, Sovie & Luskin, 2022b; Hendry *et al.*, 2023).

(2) Caveats

Some trade-offs were required in collating this data set for larger Asian vertebrates to make regional inferences. Data sources vary in quality and in the methodology used to generate the values we included in our synthesis. We sought to overcome this by triangulating results using different forms of analysis to increase confidence in the trends reported. We advise that conditions may change rapidly due to disease (e.g. African swine fever), changes in harvesting (macaque capture for medical testing) or lethal management. For example, both *S. scrofa* and *S. barbatus* populations have crashed recently due to African swine fever outbreaks across the region (Luskin *et al.*, 2023). The rapid spread of this disease could have been aided by the high population densities reported here.

VII. CONCLUSIONS

(1) The wildlife origins of the COVID19 pandemic and alarming recent work (Gibb *et al.*, 2022) show that generalist mammals persisting in human-modified ecosystems often host high pathogen loads and pose serious zoonotic disease risks, emphasising the importance of new research in these areas.
(2) We reviewed the evidence for two key generalist groups in Southeast Asia, a biodiversity and zoonotic disease risk hotspot. Specifically, we examined population trends for pigs and macaques, which are known zoonotic disease reservoirs. We show that these species are more common in most degraded areas, but the most pronounced increases – to a level we consider hyperabundant – were contingent on the nearby presence of oil palm agriculture in the landscape. This supports a dominant role of food subsidies in non-forested areas shaping wildlife outcomes inside forests, as opposed to increased foraging or habitat quality of degraded forest themselves. These results are likely generalizable to coupled human–natural environments abound across the globe (Goheen, 2016).
(3) These results can inform conservation and epidemiological work in Southeast Asia, and our approach of synthesizing camera trap data can be replicated for other species and regions.

VIII. ACKNOWLEDGEMENTS

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Forest distribution across Southeast Asia and showing percentage of forest within 2 km of an edge per country (A), the Forest Landscape Integrity Index (FLII) used in our analyses (B), the IUCN distribution maps within Southeast Asia, of wild boars (C), pig-tailed macaques (D), bearded pigs (E), and long-tailed macaques (F).

Table S1. Literature review of density estimates for long-tailed macaque, pig-tailed macaque and wild boar with corresponding Forest Landscape Integrity Index (FLII) value.

Table S2. Capture rates of long-tailed macaque, pig-tailed macaque, wild boar and bearded pig with corresponding data sources and oil palm landscape values.

Table S3. Capture rates of long-tailed macaque, pig-tailed macaque, wild boar and bearded pig with corresponding data sources and Forest Landscape Integrity Index (FLII) values.

Table S4. Covariates used for generating species abundance estimates.

Fig. S2. Study sites (A), schematic showing how habitat covariates were extracted in given radius around each camera or study centroid (B), description of the two types of scales of camera trap data reviewed (C), and the two analytical modelling approaches employed (D).

Table S5. Linear mixed model (LMM) output for individual macaque species density estimates for Forest Landscape Integrity Index (FLII).

Table S6. Study site characteristics for new camera trapping.

Appendix S1. Supplementary methods.

Fig. S3. Example from Lambir Hills National Park, Malaysia showing how camera trap locations were resampled into 0.86 km^2 hexagonal grid cells used as the sampling units in the detection history matrix in the N-mixture models.

Table S7. N-mixture modelling of estimated abundance with confidence intervals (CI) and minimum/maximum estimates for long-tailed macaque, pig-tailed macaque, wild boar, and bearded pig.

Fig. S4. Linear mixed-effects model (LMER) outputs for (A) wild boar and (B) macaque densities in response to degraded Forest Landscape Integrity Index (FLII 0 to <7) and intact (FLII 7–10) landscapes.

Table S8. Linear mixed model (LMM) outputs with relative abundance index (RAI) estimates, standard errors and statistical significance in low (<1%) and high oil palm (>20%) landscapes and intact *versus* degraded forest landscapes for long-tailed macaque, pig-tailed macaque, wild boar, bearded pig, other macaque species, and all other species.

Table S9. Total estimated relative abundance index (RAI) and percentage dominance of pigs and macaques (combined) [see Table S8 for linear mixed model (LMM) estimates] in low (<1%) and high oil palm (>20%) landscapes and intact [Forest Landscape Integrity Index (FLII) 7–10] *versus* degraded (FLII 0 to <7) forest landscapes.

Fig. S5. Box plots of relative abundance index (RAI) comparing between degraded [Forest Landscape Integrity Index (FLII) 0 to <7] and intact landscapes (FLII 7–10) for (A) wild boar, (B) bearded pig, (C) long-tailed macaque and (D) pig-tailed macaque.

Fig. S6. Box plots comparing relative abundance index (RAI) between landscapes with low (<1%) and high (>20%) oil palm cover for wild boar (A), bearded pig (B), long-tailed macaque (C) and pig-tailed macaque (D).