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Rewilding in Southeast Asia: Singapore as a case study

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Abstract

Re-establishing extirpated wildlife—or "rewilding"—is touted as a way to restore biodiversity and ecosystem processes, but we lack real-world examples of this process, particularly in Southeast Asia. Here, we use a decade of aggregated camera trap data, *N*-mixture occupancy models, and input from local wildlife experts to describe the unassisted recolonization of two native large herbivores in Singapore. Sambar deer (*Rusa unicolor*) escaped from captivity (in private or public zoos) in the 1970s and contemporary camera trap data show they have only colonized nearby forest fragments and their abundance remains low. Wild pigs (*Sus scrofa*), in contrast, naturally recolonized by swimming from Malaysia in the 1990s and have rapidly expanded their range and abundance across Singapore. While wild pigs have not recolonized all viable green spaces yet, their trajectory indicates they soon will. We also note that a third ungulate, the muntjac deer (*Muntiacus muntjak*), was captured in camera trapping in 2014 and 2015 but was never recorded afterward despite increased sampling effort, and thus we do not focus on their presumably unsuccessful recolonization. The divergent rewilding trajectories between sambar deer and wild pigs suggest different conservation outcomes and management requirements. Sambar deer may restore lost plant–animal interactions such as herbivory and seed dispersal without requiring significant management. Wild pigs, in contrast, have reached high numbers rapidly and may require active management to avoid hyperabundance and negative ecological impacts in regions, such as Singapore that lack both hunting and large predators.

KEYWORDS

Muntiacus muntjak, recolonization, restoration, rewilding, *Rusa unicolor*, Southeast Asia, urban ecology, *Sus scrofa*, tropical forest

1 | INTRODUCTION

Singapore's rapid growth into a highly developed island city-state during the 20th century radically transformed its forests and wildlife (Corlett, 1992). In the early 1900s, unrestricted hunting and the conversion of Singapore's native forests into cash crops led to the local extinction of the island's once common apex predators (tigers, leopards, and clouded leopards) (Corlett, 1992; Urban Redevelopment Authority, 1996). The influx of guns during World War II likely worsened wildlife hunting, and by the 1950s most of Singapore's wildlife >1 kg was locally extinct (Brook et al., 2003). Today only 200 ha of primary forest remains on the ~72,160 ha island city-state. However, since the late 20th century, there has been a post-independence shift in economic focus from exporting crops toward industry and an accompanying governmental campaign to create parks as natural areas amid the urban space (Tan et al., 2013). As a result, roughly 50% of the island is now vegetated (Yee et al., 2019). Although the regenerating forests and vegetated parklands host many different plant and animal species than were historically present, these areas may provide habitat for some of Singapore's previously extirpated vertebrates. This paves the way for "rewilding," a controversial method that some conservationists and land managers support to restore biodiversity and ecosystem processes (e.g., animal-mediated seed dispersal) through the natural (unassisted) or intentional (assisted, introduced) recolonization of extirpated native animals or introductions of their functional equivalents (Perino et al., 2019).

Rewilding poses challenges partly due to the lack of empirical evidence of best practices under different conditions (Perino et al., 2019). Risks of using rewilding as a conservation method include the fact that reintroduced species often lack their historic natural population controls. For example, rewilding herbivores in areas without top predators or competitors or where there are unnatural food sources may lead to hyperabundances and ecological issues, such as erosion or overgrazing (Jørgensen, 2015; Corlett, 2016). Fortunately, efforts to understand the dynamics surrounding rewilding as a conservation technique are mounting (Bakker & Svenning, 2018; Pettorelli et al., 2018; Tanentzap & Smith, 2018; Bush et al., 2022) and the focus is shifting towards acquiring more empirical data on the viability of rewilding as a conservation technique (Perino et al., 2019).

Singapore is in fact a natural rewilding experiment as large mammals that were extirpated in the last century have begun to recolonize the island, partly due to Singapore's successful regreening efforts. Now, a key conservation question for Singapore is understanding how and if the recolonizing large mammals that were once prevalent on the island will become persistent residents with sustainable population densities and what positive or negative cascading ecological effects they may trigger. An important first step in addressing this is investigating and documenting the recolonization pathways (i.e., the source, dispersal capabilities, and population growth) of the large vertebrates currently recolonizing Singapore and assessing how they are progressing across this urbanized landscape as well as what factors may shape their habitat use today.

To address this, we describe and interpret the past and present rewilding processes in Singapore for two large (> 40 kg) vertebrates: wild pigs (*Sus scrofa*, 40–80 kg) and sambar deer (*Rusa unicolor*, 80–160 kg), both of which lack population control from hunting by humans or other predators in Singapore and which may have significant ecological impacts depending on their population densities (Peel et al., 2005; Barrios-Garcia & Ballari, 2012). We leveraged available relevant news, gray literature and peer-reviewed literature and interviewed local wildlife experts and park employees to determine probable sources of recolonization and to map the historic and current dispersal of both species across Singapore. We then integrated these data with a decade of camera trap surveys to map these species' contemporary dispersal and population growth and to analyze habitat characteristics that may influence their dispersal and habitat use. This constitutes the largest (spatially and temporally) report of camera trap data across Singapore to date.

It is crucial to evaluate the population growth and dispersal of wild pigs and sambar deer during Singapore's rewilding because both species are powerful ecosystem engineers that can physically reshape ecosystems through herbivory, trampling seedlings, rooting, antler rubbing, wallowing, vegetation thinning, and other activities (Barrios-Garcia & Ballari, 2012; Bevins et al., 2014). Numerous negative ecological effects have been documented when deer and pigs reach very high densities, including decreased diversity and abundances of vertebrates and invertebrates (Barrios-Garcia & Ballari, 2012; Ivey et al., 2019), shifts in plant composition in forests through foraging and nest building (Ickes et al., 2005; Luskin et al., 2017, 2019; Luskin, Johnson, et al., 2021a), reduction of herbaceous cover, local extinction of some plants (Massei & Genov, 2004) and reduced seedling survival, damaging forests' ability to regenerate (Peel et al., 2005; Mitchell et al., 2008). In areas of overabundance, the presence of both sambar deer and wild pigs has been viewed to cause "ecological disasters" (Peel et al., 2005; Barrios-Garcia & Ballari, 2012).

Our study was exploratory in nature and our goal is to document the phenomenon of the ongoing unassisted rewilding by wild pigs and sambar deer in Singapore, which has many conservation, management, economic, and social ramifications on this densely populated island. Our work was guided by several predictions based on the ecology of the study species:

1. Limited dispersal of sambar deer and wild pigs outside of initial re-introduction sites due to Singapore's highly urban landscapes and fragmented forests.
2. Wild pigs' high reproductive rates and omnivorous diet would enable their populations to increase faster post-recolonization than sambar deer.
3. Wild pigs would show a preference for forest edges and proximity to urban areas with easy access to urban food subsidies (i.e., gardens, trash, and handouts). In contrast, sambar deer, which have relatively less tolerance for human activities and more selective herbivorous diets, would show negative habitat associations with forest edges and urban areas.
4. Finally, we did not expect to find evidence of other rewilding species because unnoticed recolonization events are unlikely on this small, densely populated island.

2 | METHODS

2.1 | Study site

Singapore has 5.8 million people (U.N. World Population Prospects, 2019) and is located just south of the tip of Peninsular Malaysia at the equator (1° 17′N, 103° 0′E). The temperatures average around 26.8 °C and the annual rainfall is ~2000 mm with two monsoon seasons (December–March and June–September) and no distinct dry season (Chia & Foongno, 1991). The island's original vegetation cover was lowland rainforest with a 40–60 m canopy dominated by trees in the Dipterocarpacae family (Corlett, 1992; Yee et al., 2019). Today, Singapore's natural areas have a range of early and late successional native species and some non-native tropical tree species (Yee et al., 2019). Such forested natural areas are almost exclusively restricted to parks and reserves on Singapore's mainland (Figure S1). Mainland Singapore's largest natural area is a group of parks collectively called the Central Catchment Nature Reserve (CCNR) located in the center of the island (Figures 1, 2). The CCNR is made up of regions separated by roads and/or water or human establishments, which influence the CCNR's connectivity for wildlife movement. The western portion of Singapore supports a relatively large natural area that is reserved exclusively for military exercises and public use is not permitted (including camera trapping or other wildlife research). This military area stretches in an oblong shape about 11 km long and 2.75 km across (Figure 1b). While there are likely wild pigs in the military area and possibly sambar deer, frequent military operations due to Singapore's diligent army program likely decrease the viability of this area as refugia for large rewilding animals. The southern edge of Singapore also has smaller natural areas shown on our maps (Figures 1b, 2a, and S1). Except for the military exercise area in the western half of the island, the camera trap studies leveraged here spanned all the largest forested natural areas in Singapore.

2.2 | Recolonization pathways, dispersal, and relative abundances across Singapore over time

We reconstructed the probable recolonization pathways of wild pigs and sambar deer in Singapore by surveying

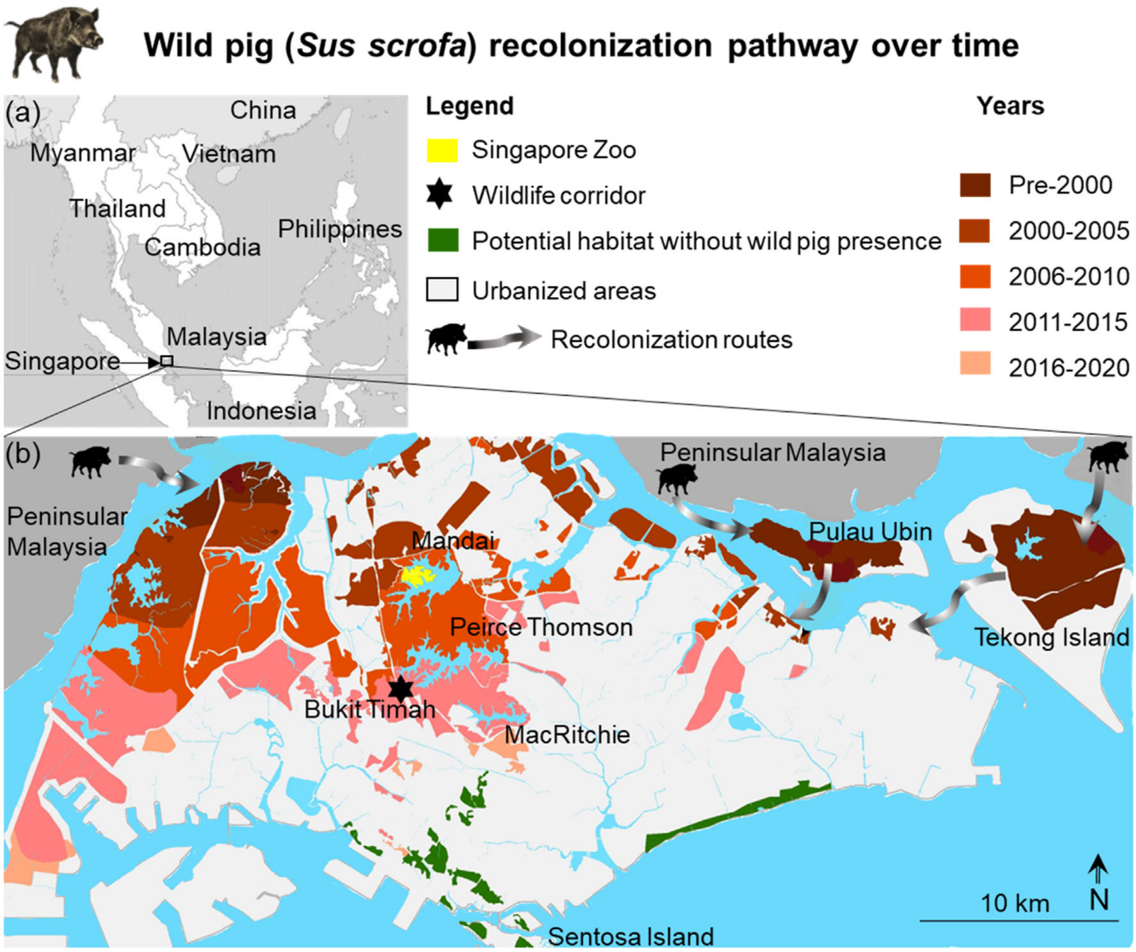

FIGURE 1 Wild boar rewilding in Singapore, reconstructed from interviews with local wildlife experts, park managers, published and gray literature, media reports, and camera trapping. (a) Singapore's location in Southeast Asia. (b) The city-state of Singapore and the recolonization pathway of wild pigs over time. Forest habitat shading denotes the timeline of wild pig recolonization, with the earliest reports in dark red and the most recent reports or camera trap detections in the lightest red. Green areas show viable habitats (forests, green spaces, or parks) lacking wild pigs detections or reports (see Figure S1 for camera trap locations).

NParks employees (Singapore's National Parks Service) and local wildlife researchers and biologists in the Singapore area (those there currently and those who had been in Singapore in previous years with relevant input). Individuals surveyed had intermediate-to-advanced experience identifying Singaporean fauna. As such, no accounts were considered uncertain or warranted being discounted. Surveys were conducted with a standardized set of questions and the information collected included the individuals' experience level and familiarity with the area of the sighting, the locations of sightings, the type of sighting (e.g., wallow, tracks, calls, direct visual), and the number of animals seen (see full survey questions in Supplementary Information S1). Next, we supplemented input provided from our surveys through a thorough search of news sources, peer-reviewed literature, iNaturalist, and Global Biodiversity Information Facility to find reports of when and where large animals were historically sighted, and relevant observations are included in our in-text citations in our Results.

We analyzed 10 camera-trapping surveys from 2009 to 2019, where a survey includes the deployment of >4 cameras for >30 days in a specific natural region (Table S1). This represents the largest collation of camera trap surveys in existence for Singapore. Occurrence information from camera trap data was integrated with our survey information (described above) to reconstruct wild pig and sambar deer recolonization and dispersal across Singapore over time (Figures 1, 2).

Most cameras were set in the CCNR and the adjacent region of Bukit Timah (Figures 1b, 2b, and S1). Camera trap brands varied among collated surveys, but all had trigger times <0.5 s, were deployed at 0.2–0.5 m height aimed at small clearings or paths and were unbaited. Camera spacing varied between surveys and so to avoid spatial pseudoreplication and to standardize analyses,

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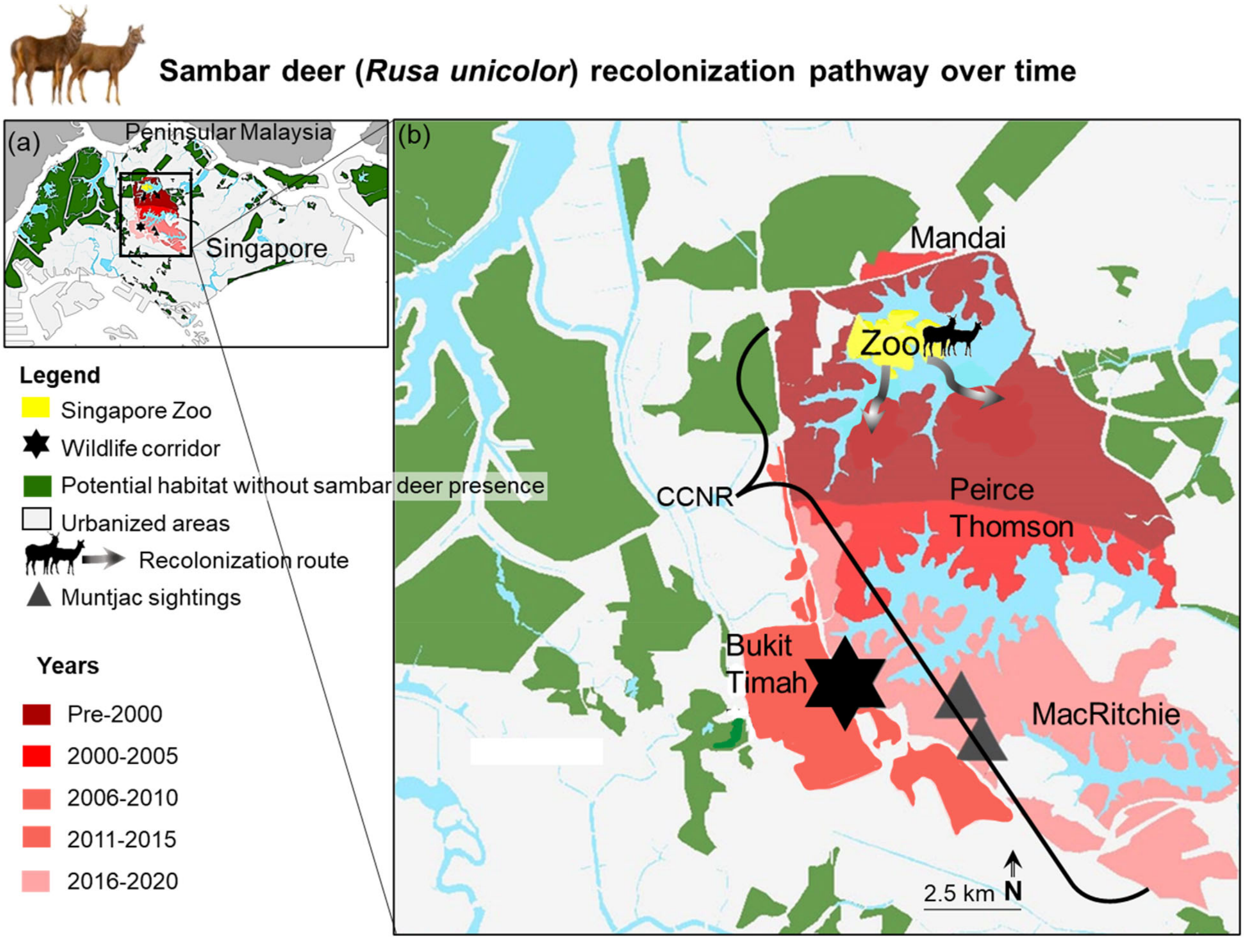

FIGURE 2 Sambar deer rewilding in Singapore, reconstructed from interviews with local wildlife experts, park managers, published and gray literature, media reports, and camera trapping. (a) Map showing the location of the Central Catchment Nature Reserve ("CCNR"; black rectangle). We note the data gap in Singapore's westernmost forest due to being a restricted and military area. (b) Enlargement of the CCNR showing the Mandai region in the north that contains the zoo, Peirce-Thomson region in the center, MacRitchie in the south, and Bukit Timah adjacent and separated by a freeway. Habitat shading denotes when the region was recolonized with the darkest reds showing the earliest reports and more recent reports or camera trap detections shown in lighter reds. Green areas show viable habitats (forests, green spaces or parks) lacking wild pigs detections or reports (see Figure S1 for camera trap locations).

camera traps were grouped into 0.22 km^2 spatial "cells" (hexagons with 250 m apothem and equivalent to camera spacing of 500–600 m) (Figure S1) and we constructed count history matrices for each cell using the total number of individuals detected in 5-day sampling windows (Darmaraj & Linkie, 2020) and accounted for differing cell sampling effort in the detection term of the hierarchical abundance models. We calculated camera deployment duration by using the dates of the first and last photos. We considered captures of the same species as independent if they were at least 30 mins apart. The detection history matrices used in our models consisted of one column per capture window and the number of rows in the matrices was the number of cells that contained one or more cameras from regions in which the focal species (sambar deer or wild pigs) was detected at least once. When individuals appeared in groups, group size was counted and incorporated into the detection matrices.

We estimated wild pig and sambar deer relative abundances separately with single-species *N*-mixture models that account for imperfect detection (R package "unmarked"; Fiske & Chandler, 2011; R Core Team, 2022). We included sampling effort as a covariate in the detection formula by summing trap nights per cell across all cameras in the cell and estimated abundance in each region per year by including a unique year *x* region covariate in the abundance formula. It is possible that animals could move between hexagonal cells (i.e., the spatial sampling unit used in our detection matrices) so the results should be interpreted as a detection-corrected relative abundance as opposed to true abundance or density. We also note that while *N*-mixture results have previously been shown to correlate with density, the relationship between them is not necessarily linear (Royle & Nichols, 2003; Duquette et al., 2014).

We also tested the influence of different habitat variables in *N*-mixture models. To do this, for each camera location, we extracted relevant habitat covariates that are known to influence vertebrate habitat use using ArcGIS (Takatsuki, 1989; Stankowich, 2008; Bonnot et al., 2013; Lamperty et al., 2021; Abram et al., 2022). These were distance to forest edges, to roads, and to the nearest urban area ("urban centers" hereafter), and the amount of the surrounding forest area within a 500 m radius that was under closed canopy forest. Preceding modeling, we assessed variables for collinearity and no significant associations between variables (see Figure S2 for correlogram). We selected best-fit models based on lowest Akaike information criterion (AIC) values obtained among models that tested all possible combinations of the four habitat variables (Table S2). The small offshore island Pulau Ubin is largely uninhabited and undeveloped but has some small areas that are inhabited. The urban areas on Pulau Ubin have a significantly lower degree of human activities (e.g., noise, traffic) relative to mainland Singapore, for example, most roads there are not paved, and urban areas are relatively small and rustic. Because of such differences between what level of human activity the covariates represent on Pulau Ubin versus mainland Singapore, we analyzed these areas separately and this is clearly labeled.

3 | RESULTS

3.1 | Wild pig recolonization, dispersal, and relative abundances through time

We received reports from 39 local wildlife experts in Singapore regarding wild pig recolonization and historical presence. There were no records of wild pigs in mainland Singapore from 1960 to 1990 and anecdotal evidence strongly suggests that wild pigs were completely hunted out of Singapore by the end of the 1950s. Experts reported the first sightings indicating recolonization had occurred along Singapore's north and north-eastern coastline in the late 1990s, suggesting wild pigs recolonized by swimming down from Peninsular Malaysia. Our reconstructed recolonization pathway and our camera trap data of wild pigs further indicate that from there, the species has continued to spread southward within Singapore (Figures 1 and 3). The initial dispersal via swimming theory is supported by the fact that wild pigs are still observed swimming in the water between Peninsular Malaysia and Singapore and its offshore islands as well as by studies on their population genetics that indicate wild pigs in Singapore came from Malaysia and have subsequently been spreading southward (Koh et al., 2018, 2019). Furthermore, Yong et al. (2010) also reported wild pigs naturally recolonized mainland Singapore in the late 1990s or early 2000s, positing they likely swam from the offshore islands of Pulau Ubin and Pulau Tekong in addition to Peninsular Malaysia. By 2010, wild pigs were documented to have a sustained presence in the CCNR (Yong et al., 2010).

Our camera trap records of wild pig relative abundances start in 2009 and show their numbers fluctuate through time (Figure 3). In the CCNR, there was a marked increase in wild pig relative abundance from 2012 to 2017, with numbers increasing as much as fourfold in some regions (Figure 3). Some of the highest estimates reach over 40 individuals in a given region, but we recommend conservatively using model estimates for discerning relative abundances rather than true density (further discussed in Methods). There was a precipitous decline in wild pig abundance from 2017 to 2020 in each of the CCNR regions (Figure 3) with no apparent cause, although a single culling event was reported from the Peirce-Thomson area, but this seems unrelated and has sparse details available (Koh et al., 2018). The island of Pulau Ubin had the highest wild pig abundance and maintained high abundances with less fluctuations than CCNR, which aligns with the common reports of wild pig sightings on the island. On mainland Singapore, wild pig abundance is highest in the Bukit Timah region to the west of the CCNR, which holds the vast majority of Singapore's remaining primary forests (Figure 3). Lastly, there are yet to be any camera trap observations in the southernmost habitats that hosted camera traps.

3.2 | Sambar deer recolonization, dispersal, and relative abundances through time

We gathered reports from 19 local wildlife experts regarding sambar deer recolonization and historical presence in Singapore. Their input, along with available literature, suggests sambar deer were extirpated in Singapore between 1940 and 1950 due to hunting and deforestation as there are no confirmed sightings from the 1940s–1972 (Teo & Rajathurai, 1997). We do note that some local experts could not rule out the possibility of a small hidden remnant population over this period. There was substantial evidence that sambar deer recolonization occurred through escape from private and public zoos in the early 1970s (Chua, 2011; Huiwen, 2019). Other reports have suggested sambar deer escaped from a local

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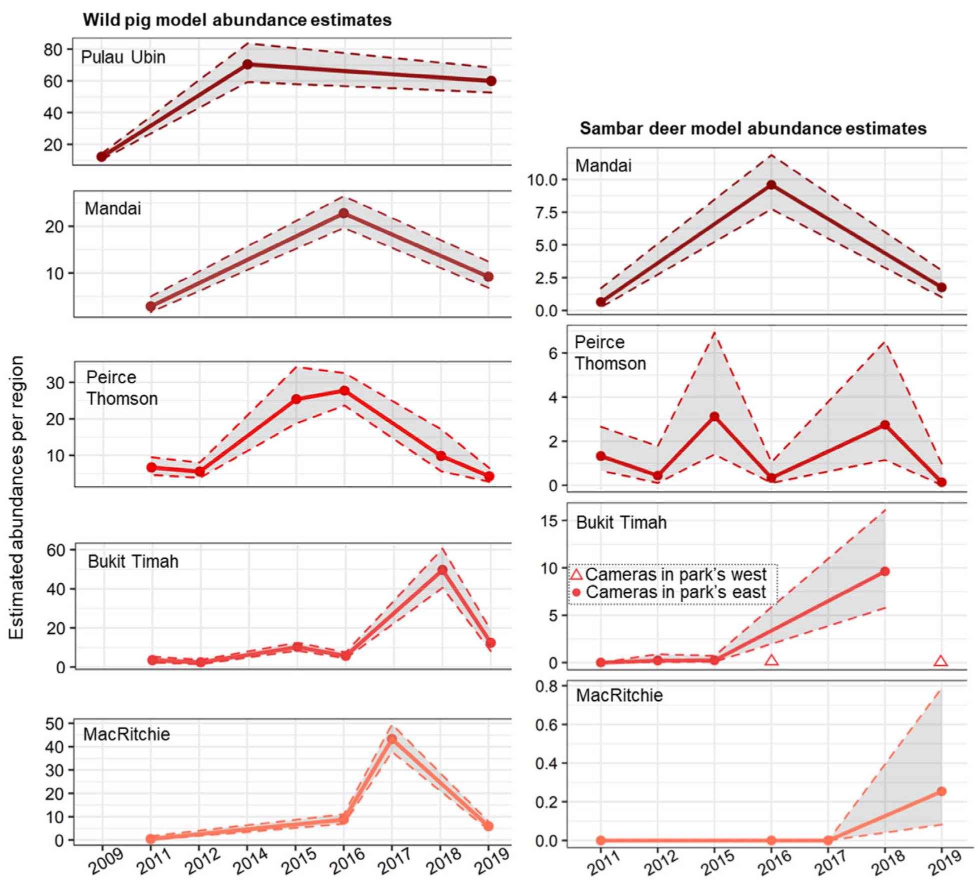
(a)



(b)

Region	Area (km²)	Overview
Pulau Ubin	10.2	Pulau Ubin is an offshore island between Peninsular Malaysia and the northeastern coast of Singapore. Pulau Ubin is rural relative to mainland Singapore. The majority of the island is undeveloped and covered by secondary forest. Results indicate pigs recolonized Pulau Ubin before mainland Singapore by swimming from Malaysia.
Mandai	11.8	Mandai hosts secondary forest and trails. Among places in Singapore with viable large-vertebrate habitat, Mandai is closest to where sambar deer likely began their recolonization of the island (the zoo). Mandai is also the northernmost region (and therefore the region closest to Malaysia) for which we have camera trap data on the mainland.
Peirce Thomson	14.7	The largest region within the CCNR (the collection of viable habitat regions of Mandai, Peirce Thomson, and MacRitchie). Peirce Thomson stretches between two reservoirs, one to its north which borders Mandai, and one to its south that borders MacRitchie. Peirce Thomson is comprised of secondary forest with some trails and grassy areas.
Bukit Timah	1.7	A small, heavily-forested region with Singapore's largest remaining primary forest fragment. This region is adjacent to the western edge of the CCNR. Bukit Timah is separated from the CCNR by a major highway over which a single wildlife corridor was built in 2013 connecting CCNR to Bukit Timah's eastern side.
MacRitchie	10.2	The southernmost region in the CCNR. MacRitchie has a small amount of primary forest and is otherwise comprised of secondary forest and grassy areas similar to Peirce Thomson. For both sambar deer and wild pigs, MacRitchie is the farthest region from their origin of recolonization into Singapore and the most recently recolonized area for which we have abundance estimates.

FIGURE 3 Population trends of recolonizing wild boar and sambar deer in Singapore's key forested habitats. (a) *N*-mixture modeling of wild boar and sambar deer relative abundance determined from camera trapping in 2009–2020. The *y*-axis is best interpreted as detection-corrected relative abundance (not absolute abundance) as individuals could move between sampling regions (see Methods and Table S1). Shaded regions represent 95% confidence intervals. (b) Forest habitat names, approximate area (rounded up to the nearest tenth km^2), and other relevant information ("Overview") where camera trap surveys have been conducted. The wildlife corridor described in Bukit Timah's overview was built to facilitate small terrestrial mammal movement and local park biologists suggest pigs and deer are unlikely to use it.

captive source (Khoo et al., 2021), potentially the Singapore Zoo which is in the Mandai section of the CCNR (Figure 2b), and the Mandai forest area is also where sambar deer were first spotted in 1973. Sambar deer were not observed outside of the Mandai forested region surrounding the zoo until the 2000s when they progressively occupied the eastern CCNR and finally began appearing in Bukit Timah in 2011 (Figures 2, 3). It is unclear how the population spread into Bukit Timah as a large highway separates the park from the CCNR.

From 2010 to 2020, camera trapping with *N*-mixture modeling suggests the relative abundance of sambar deer has remained low and fluctuated in the Mandai forested areas closest to the Singapore Zoo (Figures 2, 3). Sambar deer abundance has slowly increased within other areas of CCNR (Figure 3). In 2019, sambar deer relative abundance declined in Mandai and Peirce-Thomson, while at the same time, it appears new recolonization occurred in adjoining areas: MacRitchie to the south and Bukit Timah to the west, potentially showing a single mobile population moving out of one region into another (Figure 3). From 2017 to 2019, the newly recolonized MacRitchie area showed low but increasing relative sambar deer abundance (Figure 3). Sambar deer were detected in Bukit Timah in 2011–2012 notably only on the eastern edge, while camera traps set on the park's opposite end have yet to detect sambar deer (Figure 3). Camera traps in the southernmost portions of Singapore have not detected sambar deer.

3.3 | Unexpected detections of muntjac deer

Surprisingly, we found some information that could indicate another potential future vertebrate colonizing or recolonizing in Singapore. Muntjac deer (*Muntiacus muntjak*) has never been recorded with certainty before 2014 in Singapore, although there are some anecdotal and unconfirmed sightings in the late 1990s, supported by local wildlife expert input and literature (Teo & Rajathurai, 1997). However, we confirmed two separate muntjac camera trap capture events in the southern areas of the MacRitchie area of the CCNR, with one photo in 2014 and one in 2015 (Khoo et al., 2021). Subsequent and more intense camera trapping in the same region in 2018, 2019, and 2020 detected no muntjac deer.

3.4 | Wild pig habitat associations

For wild pigs on mainland Singapore, including habitat covariates for distance to the nearest urban area, to the nearest forest edge, and the nearest road resulted in the lowest AIC value model (Table S2). This supported our hypothesis that wild pigs are associated with urban areas (multivariate *N*-mixture model, Estimate $= -0.26 \pm 0.04$, $p < .001$***), forest edges (Estimate $= -0.29 \pm 0.03$, $p < .001$***), and roads (Estimate $= -0.28 \pm 0.04$, $p < .001$***). On Pulau Ubin, results were slightly different and the top model included forest cover, which was positively associated with wild pigs (Estimate $= 0.42 \pm 0.06$, $p < .001$***), and distance to forest edges (Estimate $= -0.31 \pm 0.04$, $p < .001$***) and to roads (Estimate $= 0.09 \pm 0.04$, $p = .04$*).

3.5 | Sambar deer habitat associations

Including both distances to the nearest urban area and distance to the nearest road resulted in the lowest AIC value when models of all possible combinations of our focal habitat variables were compared in predicting sambar deer relative abundances on mainland Singapore (Table S2). The best-fit model showed a positive association between sambar deer numbers and decreasing distances to the nearest urban centers (multivariate *N*-mixture model, Estimate $= -1.58 \pm 0.17$, $p < .001$***) and no association with distance to nearest roads (Estimate $= -0.14 \pm 0.08$, $p = .09$).

4 | DISCUSSION

Singapore's recent rewilding by two large ungulates, sambar deer and wild pigs, showed distinct recolonization pathways, dispersal capabilities, and population growth. The ability of wild pigs to disperse across a cityscape exceeded our predictions. Wild pigs have spread to a variety of forest patches across much of Singapore and, as we predicted, have quickly reached high abundances in many of the sampled regions within 20 years. This gives cause for concern because wild pigs when over abundant can trigger increased erosion and other negative ecological impacts on soils and vegetation (Barrios-Garcia & Ballari, 2012). In agreement with our predictions, sambar deer have spread more slowly than wild pigs despite having begun their rewilding journey sooner. Because sambar deer populations remain relatively small and we did not detect any signs of them becoming overabundant, we posit they do not pose an ecological threat in this setting. In fact, sambar deer may be restoring some lost ecological interactions and services such as herbivory and seed dispersal without any negative ecological impacts associated with overabundance, but this needs further investigation. Our results suggest wild pigs will need active management to control overabundance issues, while sambar deer

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may require little to no management though their abundance should continue to be monitored. Lastly, the temporary (~2 years) presence of muntjac deer that we detected indicates a failed instance of unassisted rewilding and indicates that active aid and management may be required to successfully establish a muntjac deer population in Singapore.

In reconstructing the rewilding pathways, we found wild pigs and sambar deer recolonization progressed through distinct pathways with differing successes. Historic and contemporary reports suggest that sambar deer escaped from the Singapore Zoo and colonized the adjacent Mandai forest area of the CCNR in the early 1970s. This is supported by the fact that sambar deer remain limited to the contiguous forests of the CCNR today. The sharp fall in sambar deer abundance in Mandai forest after 2016 corresponds to the clearance of ~60 ha of habitat starting in 2017 for a construction project (Lin, 2016); we posit that this could have sparked sambar deer movement out of the area and explain their gradual spread elsewhere. On the contrary, wild pigs' recolonization occurred via swimming from Peninsular Malaysia in the late 1990s. Wild pigs then spread from the northern coast inwards, and they quickly increased their numbers in most of Singapore's forest patches and seminatural parks, often crossing urban areas to do so. The only remaining unoccupied forests are in the far southern areas of the island, farthest from the recolonization areas, and we suspect these will be colonized by wild pigs in the coming decade. The decline in wild pigs from 2017 to 2019 within the CCNR is unexplained but may indicate a carrying capacity limit or disease outbreak, although no mass die-off evidence was found. We note there is no evidence of African Swine Fever in Singapore during our study (Luskin, Meijaard, et al., 2021b).

In terms of wild pig habitat associations, our predictions were supported on mainland Singapore where we found that wild pigs were associated with forest edges, roads, and urban areas. This aligns with other areas in Southeast Asia which also show high native wild pig abundances near forest edges and in fragments (Luskin et al., 2017; Love et al., 2018). This is likely because wild pigs prefer to use areas where there is a mix of human food resources (e.g., crops, garbage) as well as natural habitat resources for safety and reproduction. In particular, we suspect that females' birthing nest requirements (built of saplings in forests) are a key resource motivating wild pigs to inhabit areas relatively near forests or at least forest edges (Ickes et al., 2005; Luskin et al., 2017). In contrast to the urbanized mainland, on the small offshore and largely undeveloped island of Pulau Ubin, which we analyzed separately, only wild pigs were present (not sambar deer) and there they were strongly associated with higher forest cover which could indicate they are utilizing forest resources more so on Pulau Ubin than on the mainland. There is also significant signage on the Palau Ubin discouraging visitors from feeding wildlife which could reduce the benefits wild pigs may gain from proximity to humans compared to the mainland, further motivating more forest use relative to the mainland. Contrary to our expectations, sambar deer were associated with closer proximities to urban areas; however, we suspect this is an artifact of their limited dispersal and restricted distribution to regions on the island that are inherently closer to urban centers, rather than a true habitat preference for being closer to humans.

The disparity in the speed and degree by which wild pigs and sambar deer abundances increased after their initial rewilding journeys began has likely been driven by their differing reproductive rates. Sambar deer females begin breeding at 1.5 years of age (Dahlan & Dawend, 2013; Watter et al., 2020), mean gestation and interval between births are 260 and 329 days (Semiadi et al., 1994), and they generally have just one offspring at a time (<0.25% births) (Dahlan & Dawend, 2013). Wild pigs' growth rates are an order of magnitude higher. Wild pig females begin breeding at 8–12 months (Croft et al., 2020) and their gestation period is about 114–120 days, allowing for multiple litters of 4–6 piglets per year (though litter size depends on resource availability) (Bieber & Ruf, 2005; Frauendorf et al., 2016). In Singapore, the combination of an abundance of food sources, the absence of predators, and a complete ban on hunting to accompany an already complete lack of apex predators creates a scenario likely to foster the continued growth of wild pig populations and will almost certainly necessitate active management.

The rewilding of native extirpated wildlife may help restore biodiversity and natural ecosystem processes; however, the trajectories of species can diverge dramatically. Sambar deer have expanded slowly for 50 years in Singapore and show no immediate signs of hyperabundance and may not require active management, although we do recommend their population be monitored. Additionally, to our surprise, we found that muntjac deer appeared in Singapore recently but have since failed to re-establish. Meanwhile, the dramatic success of wild pigs in Singapore and surrounding areas highlights the potential for rewilding's double-edged sword, as any ecological benefits arising from wild pigs' rewilding will likely be quickly overshadowed by deleterious effects such as erosion and overconsumption of vegetation as the species becomes hyperabundant. Because of this, we recommend Singapore actively monitor and manage its wild pig populations. Finally, our dataset represents the largest and most comprehensive camera trap study of Singapore in terms of years spanned, the area covered, and the number of cameras, but still leaves questions about population trends as significant effort and resources are required to monitor wildlife and urban ecology, even in small habitats.

AUTHOR CONTRIBUTION STATEMENT

Idea conceived by Matthew Scott Luskin. Data collation, analysis, and writing done by Therese Lamperty with input from Matthew Scott Luskin. All other coauthors contributed to writing and data exploration, collection, and analysis.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data is available via Dryad: Lamperty, Therese (2023), Data used in "Rewilding in Southeast Asia: Singapore as a case study", Dryad, Dataset, https://doi.org/10.5061/dryad.8gtht76t5

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SUPPORTING INFORMATION

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

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