The highs and lows of serow (*Capricornis sumatraensis*): multi-scale habitat associations inform large mammal conservation strategies in the face of synergistic threats of deforestation, hunting, and climate change

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Abstract. Southeast Asia is experiencing a biodiversity crisis driven by the synergistic forces of deforestation and poaching. The mainland serow (*Capricornis sumatraensis*) is a large rainforest goat threatened by habitat loss, hunting for bushmeat, and poaching for traditional medicine. Serow have been considered to be montane forest specialists and preferring limestone karsts, but this has never been rigorously evaluated. If the species is restricted to high elevations, climate change and the upward expansion of deforestation and agriculture would threaten the species, but less so if serows are more closely associated with landscape roughness (i.e., rough topography including at low elevations such as in karst landscapes). We collated and synthesised new and existing camera-trap data from 29 landscapes across Southeast Asia to determine the serow's habitat associations at regional, landscape, and local scales. Serow occurrence was negatively associated with oil palm plantation cover and positively associated with landscape roughness across all scales; elevation was not a top-performing variable in model selection. With just 16% of their forested range under some form of declared protection, climate change and expansion of oil palm plantations into higher elevations will further reduce habitat and facilitate poaching into the species' core habitat. However, the serow's preference for rough landscapes, where mechanised agriculture is infeasible, may be its saving grace. An improved understanding of megafauna habitat associations provides conservationists, enforcement agencies, and policymakers with practical and applicable guidance to ensure their persistence in Asia.

Key words. serow, conservation, climate change, camera-trapping, occupancy modelling, habitat associations

INTRODUCTION

Deforestation, agricultural expansion, hunting, and climate change are insidious, synergistic threats undermining wildlife globally (Brook et al., 2008). The synergistic effects arise because (i) logging facilitates agricultural conversion, (ii) warming climates allow agricultural expansion to higher elevations, and (iii) the infrastructure associated with logging and agriculture enables hunters to access previously intact landscapes (Robinson et al., 1999; Symes et al., 2018).

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Deforestation and agricultural expansion have driven the conservation crisis across Southeast Asia (Symes et al., 2018; Tilker et al., 2019). The region has the highest rates of deforestation globally, largely for conversion to agriculture (Sodhi et al., 2009; Wilcove et al., 2013; Grantham et al., 2020), and the highest demands on wildlife for bushmeat and traditional medicines (Harrison et al., 2016; Gray et al., 2017).

Tropical montane forests transition from lowland forests at around 750 m elevation (Corlett, 2014). They are important reservoirs of endemic biodiversity and provides ecosystem services for millions of people in tropical regions, such as freshwater supply (Gradstein et al., 2008; Willig & Presley, 2016). Historically, logging, agricultural expansion, and hunting have primarily occurred in gently-sloping lowlands, which are more suited to agriculture, especially mechanised agriculture, leaving montane forests and montane specialist species comparatively unscathed (Edwards et al., 2014; Brodie, 2016). However, montane forest loss has accelerated during the past 20 years, with 31% of annual forest loss within Southeast Asia occurring in mountainous regions (Feng et al., 2021). The recent accelerated loss, combined with climate change, may be upending the illusion of montane forest safety. Environmental changes driven by

global warming in montane forests will disproportionately affect the distribution of mid- to high-elevation species in the region (Struebig et al., 2015; Guo et al., 2018; Zeng et al., 2018). Cool climate crops such as tea and coffee are already penetrating the highland forests (Zeng et al., 2018), and the upward expansion of timber plantations now exceeds 1,000 m elevation (Rayan & Linkie, 2020). Most concerningly, warm weather crops such as oil palm will become suitable in ~50% more of Southeast Asia's remaining forests within 50 years (Brodie, 2016). Furthermore, deforestation and oil palm will alter the local weather and microclimate that characterises montane habitats (Luskin & Potts, 2011; Chambers & Artaxo, 2017).

Megafauna restricted to montane forests and targeted by hunters may be particularly threatened. Among large (>10 kg) Asian wildlife, the mainland serow (*Capricornis sumatraensis*, hereafter just 'serow'; Fig. 1) are considered to be montane or montane-associated animals (Lekagul & McNeely, 1988; Suraprasit et al., 2020) and therefore at risk from climate change and associated effects. Serow have been recorded within landscape-specific studies to have positive associations with high elevations (>2,000 m) in Nepal and India (Aryal, 2009; Bhattacharya et al., 2012). However, this extreme elevational preference is less applicable to Southeast Asia, which has very few areas >2,000 m in elevation and where the species is often recorded at mid-elevations (500–1,500 m) (Phan et al., 2019; Bakri et al., 2020) and as low as 200 m in Sumatra (Santiapillai, 1997). Alternatively, serow have been associated with rough terrains such as limestone karsts or rocky outcroppings that the species is reported to use as a refuge (Lekagul & McNeely, 1988; Clements et al., 2006; Lynam & Round, 2006; Susanti et al., 2006). This suggests that the species may not be strictly high elevation-associated but associated more with rugged terrain and less acutely threatened by climate change if it persists in lower elevations. Phan et al. (2019) found that serow occupancy was more strongly positively related to the steepness of terrain than elevation. A study from Nepal found that serow were not detected within unprotected areas in the mid-elevation ranges (1,400–2,600m) but were still present in protected lower elevation areas and inaccessible higher elevations (Paudel & Kindlmann, 2012). Serow also exhibit higher occupancy with further distance from human presence (Bhattacharya et al., 2012; Paudel et al., 2015; Phan et al., 2019). Across their wide range, serow have been recorded in subalpine, montane, temperate, and tropical forests (Groves et al., 2015; Phan et al., 2020). Based on isotope analysis, Suraprasit et al., (2020) suggested that during the Pleistocene, serow in Thailand were more generalist, open-landscape species than the closed-canopy forest-associated species they are recognised as presently.

The utilisation of the serow is less widely known than more charismatic Asian mammals. Serow are actively targeted by hunters for their meat, for medicinal uses, including bile from the gall bladder and oil made from the preorbital facial glands, and as a trophy (Lynam & Round, 2006; Shepherd & Krishnasamy, 2014; Leupen et al., 2017; WWF,

2017; WWF, 2020). Hunting has been a key factor driving a >30% decline in serow population size over the last 10 years, earning the species a Vulnerable categorisation by the IUCN Red List (Phan et al., 2020). Despite serow being listed under Appendix 1 of CITES (The Convention of International Trade in Endangered Species) and having strong legislative protection across the majority of its rangeland states (notable exceptions are Myanmar and Cambodia), the serow is still highly sought after for trade, and enforcement seems rare (Phan et al., 2020). Serow also play important an role in the regions food web for carnivores (Amir et al., 2022a, 2022b), especially after the loss of wild pigs from African swine fever (Luskin et al., 2020, 2023). Given the threats affecting the serow, the lack of reliable data on the distribution and abundance of this species impacts the ability to identify habitat associations and conservation priorities (Phan et al., 2020; Chen et al., 2021).

In this study, we provide a synthesis of habitat associations of serow within Southeast Asia, utilising a multi-scale study. We leveraged data from 16 new camera-trapping sessions across seven landscapes, as well as peer-reviewed, published camera-trapping studies, and occurrence records from the Global Biodiversity Information Facility (GBIF) database (GBIF, 2021). Consistent with previous reports, we hypothesised there would be a positive association with elevation that peaks in montane forest elevations (i.e., >750 m) and a positive association with landscape roughness, as the species is often reported from limestone karsts (Lekagul & McNeely, 1988; Suraprasit et al., 2020). We hypothesised that serow are negatively associated with anthropogenic factors indicative of hunting pressure, such as human populations and agriculture (Leupen et al., 2017; Symes et al., 2018). We used three approaches to understand the habitat associations of the serow across multiple scales: (i) Maxent presence-only modelling to map the probability of occurrence at the regional scale, (ii) generalised linear mixed-effects models (GLMMs) to understand variation in the number of independent detections reported in published camera-trapping studies and new camera-trapping sessions at the landscape scale, and (iii) hierarchical abundance modelling using our new camera-trapping sessions, which accounts for detectability, to assess variation in the relative abundance of serow at the local scale. Through the use of a multiple-scale analysis from broader to finer scales, we are able to determine whether serow's habitat preferences are similar when looking at variation across the region (e.g., low-lying versus mountainous parks) compared to variation within-landscapes due to habitat conditions (e.g., valleys versus ridges) (Wu et al., 2009).

MATERIAL AND METHODS

Study species. The mainland serow (*Capricornis sumatraensis*) (Fig. 1) has three recognised subspecies across its extensive range in Asia (Phan et al., 2020; Table 1). Previously, each was considered a unique species until a recent mitochondrial genome analysis reclassified them into

Table 1. Distribution of the three subspecies of mainland serow (*Capricornis sumatraensis*). Until recently, these were each considered unique species; however, mitochondrial genome analysis regrouped them into a monotypic species (Mori et al., 2019). Adapted from Phan et al. (2020).

Subspecies	Distribution	Range Description
C. s. sumatraensis	Indonesia (Sumatra), Peninsular Malaysia, & Thailand.	South of about 9° N latitude, approximately to the Isthmus of Kra in Thailand, down the Malay Peninsula in forest patches, and then restricted to the Bukit Barisan Mountain range in Sumatra, Indonesia.
C. s. mildneedwardsii	Myanmar, Cambodia, China, Lao PDR, Thailand, and Viet Nam.	Extends from the eastern Himalayas and Indo-Burma, Southern and Central China, across mainland Southeast Asia, down the Thai/Malay Peninsula until the Isthmus of Kra.
C. s. thar	India, Nepal, Bhutan, Bangladesh	Confined to the Himalayan Ranges.

Fig. 1. Camera-trap image of mainland serow (*Capricornis sumatraensis*) from the lowlands of the Pasoh Forest Reserve in Peninsular Malaysia at an elevation of ~100 m.

a single monotypic species (Mori et al., 2019). Our study reflects this and analyses data to the species (*C. sumatraensis*) level, but limited to its Southeast Asian range.

Data Collection. We compiled data from three sources: (1) camera-trapping studies in published literature, (2) new camera-trapping sessions carried out across the focal region and (3) the Global Biodiversity Information Facility database (GBIF, 2021), a global repository of biodiversity data including museum records and citizen science reports.

We identified published camera-trapping studies using the key terms 'Sumatra', 'Peninsular Malaysia', 'Thailand', 'Laos', 'Cambodia', 'Vietnam', 'Myanmar', and the term 'camera trap'. A published 'study' was defined as data from a continuous sampling effort using >5 cameras within a landscape (10–1,000 km²). We included studies that reported sampling efforts and the number of detections conducted after the year 2000. Snowball sampling was done by examining references in key papers from the initial search. The location (forest name and coordinates), independent captures of the species, and effort data were collected from each study. We refer to the area sampled as a 'landscape', which was usually a national park or other protected area, production forest, or collection of forest patches within a 1,000-km²

area. We grouped multiple studies from the same landscape per year by summing captures and effort among the studies and averaging the covariate values (See Table 2 for a full list of covariates).

For the new camera-trapping, we conducted 16 sessions in seven landscapes across areas ranging from 10 to 813 km² (Dehaudt et al., 2022; Dunn et al., 2022, Hendry et al., 2023) (Fig. 2). We did not include Singapore since recent work established they remain extirpated despite two other large ungulates recolonising (Lamperty et al., 2023). We deployed between 18 and 112 passive infrared Bushnell and Reconyx brand camera traps at each landscape (Table 3). Each session used standardised methods, attaching the camera traps 0.2–0.3 m above ground in trees along hiking trails or natural wildlife trails. Cameras were deployed for approximately 60–90 days at each landscape from December 2013 until March 2019 and we considered detections independent if they occurred at least 30 minutes apart (Rovero & Zimmermann, 2016). Cameras were systematically deployed within pre-mapped grids, at least 500 m apart in large forests (>100 km²) and 100–500 m apart in smaller forest patches. To prevent spatial pseudo-replication and to ensure that model outputs were spatially comparable across multiple landscapes, the capture data from specific cameras was resampled into 0.86-km² hexagonal grid cells (short diagonal of 1-km), hereafter called a 'sampling unit' following Rayan & Linkie (2020). We averaged covariate values when multiple cameras fell within the same sampling unit. We produced a detection history matrix using presence/absence data from all sampling units and used a sampling occasion window of five days to increase detection probability and reduce the number of zeros (0 = species not detected; 1 = species detected; NA = inactive sampling unit or occasion).

Mapping range and probability of presence at the regional scale. We calculated the remaining potential habitat of the serow and its probability of presence within this range. We first took the current extent of occurrence (EOO) as the total area (km²) of the IUCN-recognised range of the serow within Southeast Asia (extracted from Phan et al., 2020) and then calculated the area of occupancy (AOO), which is defined as the forested area remaining (km²) within the EOO in 2015 (Miettinen et al., 2016). We also calculated the percentage of protected forest within the serow's Southeast Asian range

Table 2. Description and sources of spatial data used in our analyses.

Covariate Type	Covariate source, description, or calculation	Year	Resolution	Source hosting the layer
Forest cover	Natural tree cover (excluding plantations)	2015	1 km	Miettinen et al. (2016)
Forest edge	Distance to forest edge	2015	1 km	Miettinen et al. (2016)
Oil palm	Industrial plantations only, likely captures a minority of total oil palm	2015	1 km	Miettinen et al. (2016)
Pristine forest	Combined land cover of lowland evergreen forest, lower montane evergreen forest, lowland deciduous forest, lower montane evergreen forest, and ultramafic evergreen forest.	2015	1 km	Miettinen et al. (2016)
Degraded forest	Combined land cover of oil palm, lowland mosaics, lowland open ground, and regrowth/plantations	2015	1 km	Miettinen et al. (2016)
Forest integrity	Forest Landscape Integrity Index capturing direct and indirect pressures on forest.	2020	300 m	Grantham et al. (2020)
Elevation	SRTM Digital Elevation	2020	30 m	https://dwtkns.com/srtm30m/
Land cover	MODIS classification system	2015	250 m	Miettinen et al. (2016)
Human density	Human settlements and population later	2015	250 m	https://ghsl.jrc.ec.europa.eu/
Settlements	Overpass Turbo - OSM	2020	vector	http://overpass-turbo.eu/
Roads	OpenStreetMap	2020	vector	https://www.openstreetmap.org
Rivers	GRIN - Global River Network	2017	vector	https://www.metis.upmc.fr/en/node/375
Human footprint	Human Footprint Index showing cumulative human pressures from direct and indirect sources.	2009	1 km	Venter et al. (2016)
Country boundaries	Country Boundaries	2020	vector	https://gadm.org/download_country_v3.html
Night lights	DMSP-OLS Night-time Lights	2013	1 km	https://eogdata.mines.edu/dmsp/
Forest Loss	Forest Change 2000–2019	2019	30 m	Hansen et al. (2013)
Landscape Roughness	Degree of irregularity of the surface	2017	1 km	Fick & Hijmans (2017)
Slope	Angle of inclination to the horizontal	2017	1 km	Fick & Hijmans (2017)
Protected areas	IUCN and UNEP-WCMC, The World Database on Protected Areas (WDPA)	2017	vector	www.protectedplanet.net

[as recognised from the Protected Planet database (UNEP-WCMC, 2021)].

The probability of presence of the serow within its Southeast Asia range was then mapped using Maxent software (Version 3.4.1) (Phillips et al., 2021). This tool uses presence-only data with spatial covariates (Phillips & Dudík, 2008). All occurrence records from the three data sources were used. We limited our analysis to records after the year 2000 to limit the chance of recording areas where the species may have been recently extirpated from. Eight spatial layers (elevation, landscape cover, mean annual rainfall, forest cover, forest integrity, distance to edge, landscape roughness and slope) were used for extracting covariates, as well as three anthropogenic spatial layers (human population density, nightlights, and oil palm plantations), totalling eleven covariates (Table 2). When geographic coordinates of species presence were unavailable, we used the coordinates of the centroid of the specified study area or forest patch as indicated in the paper.
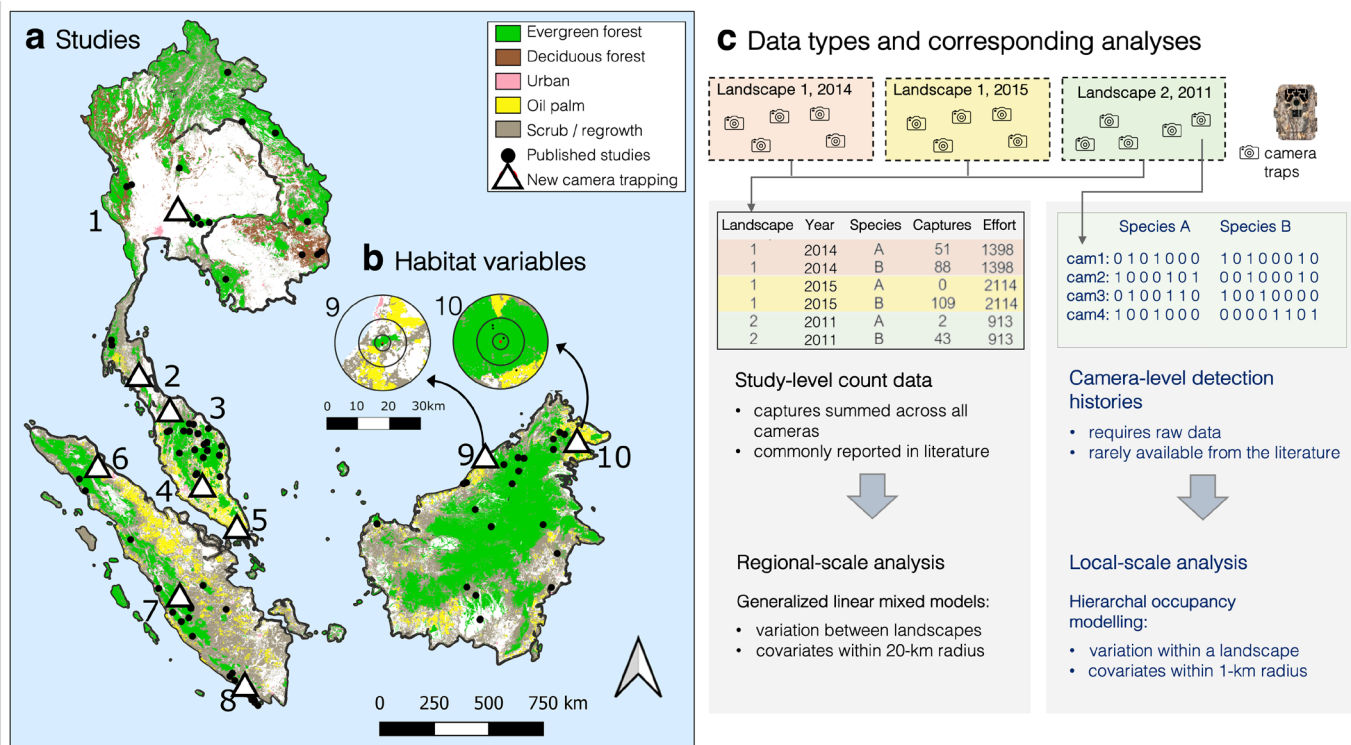
Fig. 2. Study area and diagram of camera-trapping data types and analyses. Inset (a): Study sites where camera-trapping was undertaken, with black circles showing where published camera-trapping sessions were located and red circles showing locations where new camera-trapping was conducted. The left side of panel (b) shows the structure of the study-level number of detections per landscape that was analysed using Poisson GLMMs. The right side of panel (b) shows the camera-level detection histories that were used in hierarchical abundance modelling. Inset (c) summarises the data flow from the landscape-level captures reported by published studies used in GLMMs versus the camera-level detection histories used in the hierarchical abundance modelling. Schematic adapted from Decœur et al., 2023.

Maxent offers a wide variety of setting options which occasionally requires species-specific settings and allows for a study-specific adjustment (Merow et al., 2013). Therefore, we ensure that the setting options were adjusted to our specific study aims and our intended assumptions (Peterson et al., 2011; Merow et al., 2013). The adjusted parameters were as follow: (i) Convergence threshold was set to 1×10^{-6} to lower the omission rate (Jobe & Zank, 2008); (ii) The number of replicated runs was set to ten times (the averaged value is the one used as the result) using "cross-validate" as the replicated run type. Using "cross-validate" means to split the data ten times (10% per partition), train the model ten times on 90% of the data, and test it each time on the 10% partition alternately (Merow et al., 2013); (iii) Maximum iterations were set to 5,000 for each run to allow the model to have adequate time for converging; (iv) Doubled the "regularisation multiplier" value to reduce over-fitting (Radosavljevic & Anderson, 2014); (v) Feed the setting with bias file to represents the sampling effort across the study area and to limit areas for Maxent to extract background (pseudo-absence) data with a maximum number of 5,000 (Barbet Massin et al., 2012; Kramer Schadt et al., 2013; Fourcade et al., 2014; Stolar & Nielsen, 2015). Bias file is a probability surface that represents the intensity of sampling effort across the area of study and gives a gradual weight to random background data used for modelling (Fourcade et al., 2014). We created bias grids by deriving a Gaussian kernel density map of the occurrence locations using SDMToolbox

of ArcGIS, and then rescaled it from 1 to 20 (Brown, 2014; Fourcade et al., 2014).

A jackknife test was run to estimate the relative contribution of each variable to the model. A cloglog output format was used to generate a map serow probability of presence estimated based on the spatial layers. The Maxent-generated probability of presence was then mapped within the area of the remaining forest in the species' range (AOO). For visual interpretation purposes, we turned off the "Logscale pictures" to provide a linear scale on the produced Maxent map picture.

Habitat associations assessed using camera-trapping at the landscape scale. We investigated serow habitat associations by analysing how the number of independent captures in each study area varies due to several environmental and anthropogenic factors using data from published camera-trap studies and new camera-trap sessions. The sampling unit was each landscape, where we combined the total number of independent captures of serow from all cameras in the study. To account for multiple studies from the same landscape, we subdivided our data for each landscape by year, summing captures and effort among studies and averaged the covariates. Each landscape was assigned a value for 8 different habitat variables of interest: forest patch size, average elevation, landscape roughness, forest intactness, forest cover, forest integrity, human population, oil palm and human footprint.

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Table 3. Study site description, effort, and success for the 16 new deployment sessions. Average annual rainfall from 1970–2020 (Fick & Hijmans 2017) was extracted over a radius around the geographical centroid of a survey. Multiple surveys that used different cameras within a single landscape may have slightly different annual rainfall. Trap nights were estimated from the first and last photos taken for each collected camera. MCP refers to the minimum convex polygon around the camera traps. Naïve occupancy was the number of cameras that detected the species. Detections were independent events (>30 min rest period between photos of the same species). The relative abundance index (RAI) is calculated as the number of independent photos per 100 trap nights.

Region/landscape	Year	Annual rainfall (mm)	Session period	Number of cameras	Effort (trap nights)	Elevation (Mean ± SD)	Elevation range	MCP	Camera spacing	Naïve camera-level Occupancy	Independent Captures	RAI - Captures per 100 trap nights
THAILAND												
Khao Chong / Khao Ban Tat	2018	2014.28	1 February 2018–30 April 2018	76	3957	524.59 ± 270.92	103–1,234	59.01	467.95	0.045	5	0.126
Khao Yai	2019	1119.49	1 July 2019– 25 September 2019	61	3553	769.64 ± 38.56	582–816	22.54	464.42	0.032	1	0.028
SUMATRA												
Gunung Leuser	2014	2828	18 December 2013–22 May 2014	69	3401	316.03 ± 250.38	25– 88	516.15	1275.27	0.145	20	0.588
Kerinci Seblat	2014	2406.94	10 February 2014–4 October 2014	98	5356	594.03 ± 194.46	252–1,154	813.69	1169.04	0.054	3	0.056
Bukit Barisan Selatan	2014	2987.8	15 June 2014–20 September 2014	79	5750	369.75 ± 184.97	116–935	473.58	1139.96	0.064	5	0.087
PENINSULAR MALAYSIA												
Pasoh	2013	2081.4	29 May 2013–12 February 2014	58	1399	297.09 ± 160.10	98–674	133.53	1316.26	0.034	2	0.143
	2014	2079.16	13 May 2014–1 August 2014	57	1314	303.14 ± 160.04	98–674	134.62	1321.48	0.035	4	0.304
	2015	2079.78	7 May 2015–4 September 2015	59	1670	301.15 ± 158.15	98–674	134.62	1317.78	0.034	2	0.12
	2017	2086.38	17 May 2017–29 August 2017	42	1305	308.98 ± 156.05	103–674	122.63	1416.43	0.048	2	0.153
Ulu Muda	2015	2057.03	1 November 2014–30 January 2015	76	4242	278.58 ± 128.68	117–628	68.98	938.65	0	0	0
	2015	2063.01	31 January 2015–1 May 2015	112	4446	295.77 ± 139.83	117–843	113.61	731.56	0	0	0
	2015	2080.9	2 May 2015–31 July 2015	52	3582	325.38 ± 166.15	141–843	115.53	1227.86	0	0	0

Region/landscape	Year	Annual rainfall (mm)	Session period	Number of cameras	Effort (trap nights)	Elevation (Mean ± SD)	Elevation range	MCP	Camera spacing	Naïve camera-level Occupancy	Independent Captures	RAI - Captures per 100 trap nights
	2015	2078.17	1 August 2015–30 October 2015	48	2862	328.92 ± 165.27	123–843	104.01	1237.85	0.021	1	0.035
	2016	2065.89	31 October 2015–29 January 2016	73	2220	313.62 ± 145.27	117–748	103.17	794.92	0	0	0
	2016	2054.55	30 January 2016–29 April 2016	60	2899	285.45 ± 135.12	117–628	66.96	958.39	0	0	0
	2016	2060.54	30 April 2016–22 July 2016	46	2746	301.30 ± 138.91	117–628	65.72	974.47	0	0	0

For most of these habitat variables, we extracted them at 1-km² resolution and calculated the sum or average values (Table 2) within a 20-km radius around the centroid of cameras for each landscape. Only forest patch size was not restricted by a zone around landscapes. GLMMs with zero-inflated Poisson error distribution were used to analyse the landscape-level count data. Study effort (measured in trap nights) was controlled for as a fixed effect covariate and landscape as a random effect to account for multiple years of camera-trapping within the same study or multiple studies within the same landscape. There was unexplained variation in captures, given differences in equipment and the deployment methodologies amongst studies. These sources of error may reduce the modelling power, and chances of detecting "true" significant relationships (Sollmann et al., 2013).

Competing models with combinations of covariates were compared using an information-theoretic approach and evaluated using Akaike Information Criterion (AIC) corrected for small sample size (AICc) and model weights based on AICc (Burnham & Anderson, 2002). We also tested quadratic relationships in addition to the first-order terms for landscape roughness, elevation, slope, tree cover, and forest integrity due to past research suggesting serow habitat preferences may have led to non-linear relationships with these variables. (Lekagul & McNeely, 1988; Clements et al., 2006; Lynam & Round, 2006; Aryal, 2009; Bhattacharya et al., 2012; Groves et al., 2015; Paudel et al., 2015; Phan et al., 2019; Bakri et al., 2020, Suraprasit et al., 2020). We considered the best model to have the lowest AIC score, and models within 2 AIC units of the best model were considered competitive with the best model. All GLMMs were fitted with the R package "GLMMadaptive" (Rizopoulos, 2019) in R version 4.0.3 (R Core Team, 2020). We tested for but did not find strong correlations between any covariates (i.e., Pearson's correlation coefficient $|r| < 0.5$).

Relative abundance relative to spatial covariates at the local scale. We assessed how serow local abundance was affected by local habitat covariates using data from our new camera-trapping sessions in Royle-Nichols (RN) abundance modelling that accounts for imperfect detection (Royle & Nichols, 2003). We tested if the relative abundance of serow within landscapes varied with elevation, distance to river, forest cover, forest integrity, distance to forest edge, human footprint, human population, oil palm plantations, landscape roughness (Table S1). Unlike our landscape-scale GLMM analysis, we did not consider quadratic relationships at the local scale due to the smaller sample size generated in the new camera-trapping sessions. We compared competing hypotheses using the AIC information theoretic approach described above. All RN abundance models were implemented in the R package "unmarked" (Fiske & Chandler, 2011). In all models, we included the camera-trapping session identifier as an abundance covariate to account for landscapes having multiple camera-trapping sessions and to maintain the spatial and temporal independence of our sampling units to satisfy population closure assumptions in the model. We also included the

Table 4. Sources of data and sample sizes that were used for this study's three analyses: (1) camera-trapping (CT) studies in published literature, (2) new camera-trapping sessions carried out across the focal region and (3) the Global Biodiversity Information Facility database (GBIF, 2021), a global repository of biodiversity data including museum records and citizen science reports.

Analysis & Source	Records
Presences for Maxent modelling (Total)	**49**
Published CT: 25 studies in 21 landscapes	21
New CT: 16 sessions at 7 landscapes	7
GBIF online repository	21
CT observations for GLMMs	**253**
47 surveys (25 w/ detections) at 29 landscapes (21 w/ detections)	
Independent captures for abundance modelling	45
New CT: 16 sessions (10 with detections) at 7 landscapes (7 with detections)	

Table 5. Serow range and study effort within Southeast Asia. The Extent of Occurrence (EOO) is calculated as the total area of the IUCN range in each region (km²). The Area of Occupancy (AOO) is defined here as the forested area remaining (km²) within the EOO in 2015 (Miettinen et al., 2016). Note this is an overestimate as it assumes all remaining forest is occupied. The AOO may be more correctly interpreted as the remaining habitat available for serow. The remaining 'Forested Area' is the AOO divided by the EOO and presented as a percentage. The percentage of protected area is the forested area within protected areas divided by the AOO. Protected areas were taken from the Protected Planet database (UNEP-WCMC, 2021). A value of NA for effort, cameras, studies, etc indicates that we did not find any published camera trapping studies that detected serow from these countries.

Region	EOO (km²)	AOO (km²)	Forested Area (%)	Protected Area (%)	Total Cameras	Effort (Camera trap nights)	Number studies with detections	Number of studies without detections
Cambodia	13,086	8,286	63.3	62.2	210	18,248	1	1
Laos	217,444	102,574	47.2	13.6	298	4,344	1	0
Myanmar	513,736	288,018	56.1	6.6	NA	NA	NA	NA
Thailand	259,282	109,131	42.1	27	485	53,973	6	3
Vietnam	19,218	13,970	72.7	61.7	NA	NA	NA	NA
Sumatra	105,369	62,252	59.1	24.7	897	80,916	12	8
Peninsular Malaysia	25,848	17,248	66.7	25.7	1,517	110,644	10	5
Southeast Asia (total)	1,153,999	601,483	52.1	16.1	3407	268,125	30	17

number of trap nights as a detection probability covariate to account for differing sampling effort per sampling unit.

RESULTS

Occurrence and camera-trap records. We collated a total of 680 geo-referenced occurrence records of the serow. This included 614 independent captures from 25 published camera-trap studies (see Appendix), 45 independent detections from new camera-trapping sessions (total effort = 50,702 camera trap nights), and 21 occurrence records from GBIF (Table 4). Our new camera-trapping sessions included 1,066 cameras that were set across 7 landscapes in Thailand, Peninsular

Malaysia, and Sumatra (Fig. 2, Table 3). The highest number of detections within a single session (20) and highest relative abundance index (0.588 photos per 100 trap nights) was at Gunung Leuser National Park (Table 3). The Ulu Muda landscape in Peninsular Malaysia only yielded a single serow detection despite the largest trapping effort (total of 22,997 camera trap nights across 7 sessions).

Regional scale range and probability of presence. We obtained 49 geo-referenced occurrence records of serow for our Maxent probability of presence analysis (Table 4; Fig. 3a). The EOO of the serow was 1,153,999 km² within Southeast Asia (including the countries listed in Table 1 and excluding non-Southeast Asian countries within the serow's

(a) Occurrence reports

(d) Forest area within IUCN range

(e) Probability of presence in remaining forest

(b) Variable performance in Maxent
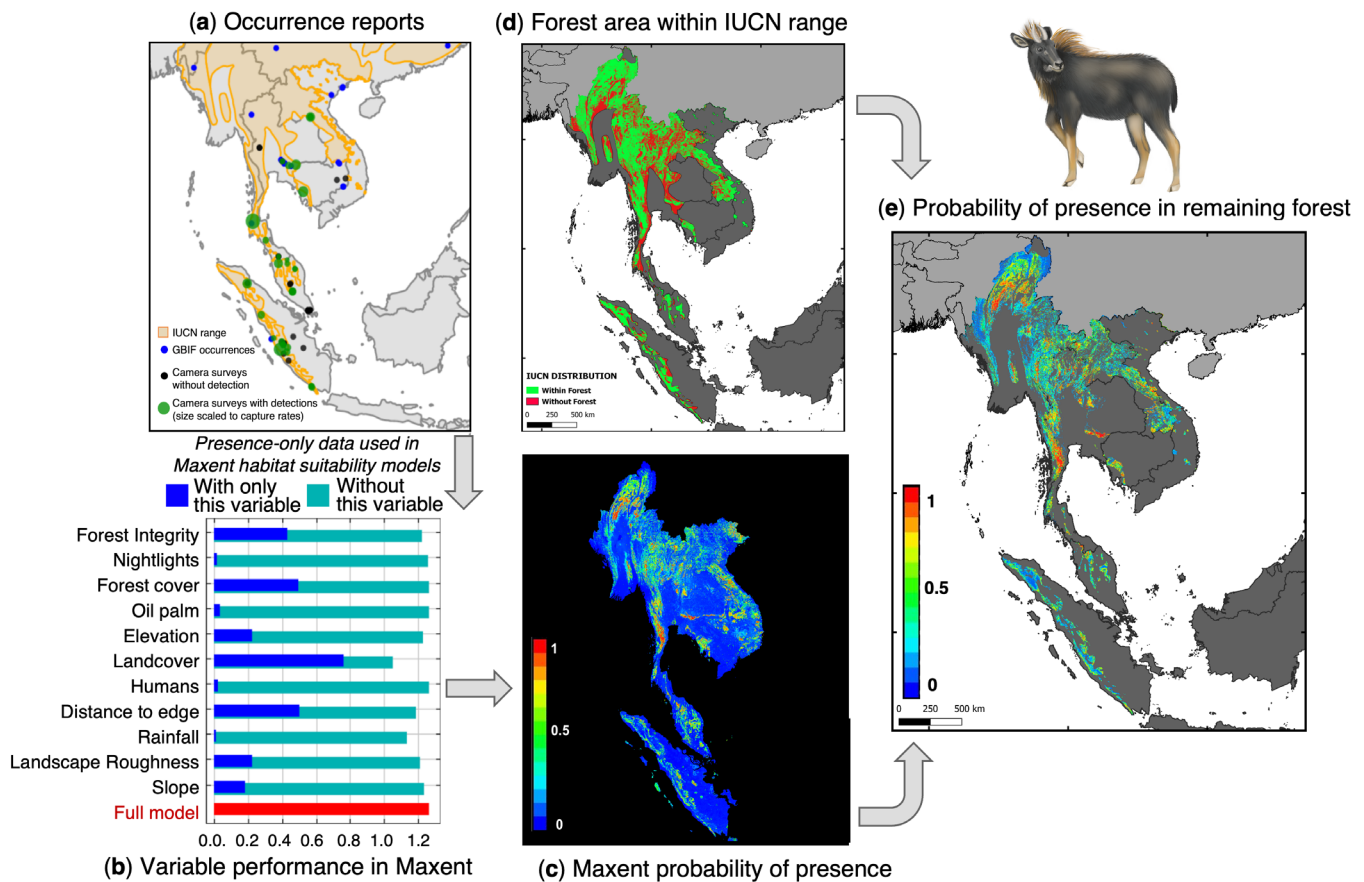
(c) Maxent probability of presence

Fig. 3. Presence of the serow within its Southeast Asian range. Panel a) shows the IUCN Red List range extent of occurrence (EOO; shaded orange), and the occurrence records coloured by the data source. Panel b) shows the jackknife-based assessment of variable importance. The blue bars showing the explanatory power in the model using only the denoted variable, while the teal bars show the predictive power of the full model without the denoted variable, highlighting whether the variable captures unique information. Panel c) shows the probability of presence of the serow from Maxent modelling mapped within the Southeast Asian region covered by this study. Panel d) shows the forest cover in 2015 that is potentially occupied within the EOO. Panel e) is the Maxent probability of presence of serow inside the remaining forested areas within Southeast Asia. Original artwork courtesy of Tamzin Barber (https://www.talkinganimals.com.au/).

range including Bangladesh, Bhutan, China, India, & Nepal). We calculated AOO to be 601,483 km², or 52.1% of the recognised IUCN range (Table 5, Fig. 3d.). Furthermore, only 16.1% of the AOO of the serow fell within protected areas. Total study effort can be found in Table 5.

Our Maxent analysis of the serow's Southeast Asian range had a mean value of AUC 0.915, which demonstrated that the model performed well and had good discriminatory ability between variables (Peterson et al., 2011). We adjusted the Maxent settings for our specific study aims and assumptions, including an established process to reduce sampling bias (Peterson et al., 2011; Merow et al., 2013). We used the "cloglog" output format to retrieve the probability of presence, which is linearly scaled between 0 (lowest) to 1 (highest) (Phillips, 2017). We ran a jackknife test to estimate the variable importance of the regularised training gain, and test model performance using the receiver operating characteristics through partitioned test data from the "crossvalidate" replicated run type setting (Phillips et al., 2009). The evaluation of Maxent models can be a challenging task, and some discussions have indicated that AUC (Area Under the Curve) may not always offer useful information to effectively assess and evaluate model performance (Lobo et al., 2008; Jiménez-Valverde, 2012; Bahn & McGill,

2013). We reported AUC to illustrate that the continuous probability model outperforms other models. (For specific adjusted Maxent parameters, see details in Appendix M1). Serow had a medium to high probability of presence (≥ 0.8) in areas with higher elevations such as the Annamite Range on the border of Laos and Vietnam continuing south until the border of Cambodia, the Tenasserim and Dawna Ranges that form the border between Thailand and Myanmar, and Khao Yai National Park, Thailand. The Barisan Mountains of Sumatra, and Peninsular Malaysia had probability of presence of around 0.5 (Fig. 3c). The Maxent jackknife metric showed land cover type was the most important variable (Fig. 3b).

Landscape scale habitat associations of serow. The GLMMs utilised data from 47 studies across 29 landscapes (Table 4). The top multivariate GLMM included a negative effect of oil palm cover (β = -2.429 SE = ±0.366) and positive effect landscape roughness (β = 1.923, SE = ±0.193) (Fig. 4, Table 6).

Local scale predicted abundance of serow. We assessed local variation in serow abundance using hierarchical RN abundance models that account for detection probability. The best performing model based on AICc was a multivariate model that included a negative effect of oil palm (β = -1.268,

Table 6. Model selection and performance of Generalised Linear Mixed-effects Models assessing the habitat variables predicted to influence trapping success. All models included the number of independent detections as the response variable and random effects for trapping effort and study site (N = 47 studies from 29 landscapes). Only models performing better than the null are shown.

Model	AICc	ΔAICc	AICwt
~Roughness + oil palm	285.09	0	0.74
~roughness^2 + oil palm	287.82	2.73	0.19
~Elevation^2	347.09	62	0
~Roughness	354.02	68.94	0
~Forest Integrity + roughness	354.37	69.28	0
~Forest Integrity + oil palm	398.47	113.38	0
~Forest integrity + elevation	406.91	121.82	0
~Roughness^2	414.07	128.99	0
~Tree Cover	418.17	133.09	0
~Elevation	422.59	137.5	0
~Elevation + oil palm	423.34	138.25	0
~Human Footprint Index + elevation	425.76	140.68	0
~Oil palm	426.07	140.99	0
~Tree Cover	426.58	141.49	0
~Human Footprint Index + oil palm	427.93	142.85	0
~Forest Integrity^2	429.81	144.73	0
~Forest Integrity	431.26	146.17	0
~Slope	435.53	150.45	0
~Slope^2	435.53	150.45	0
~Null	435.66	150.57	0
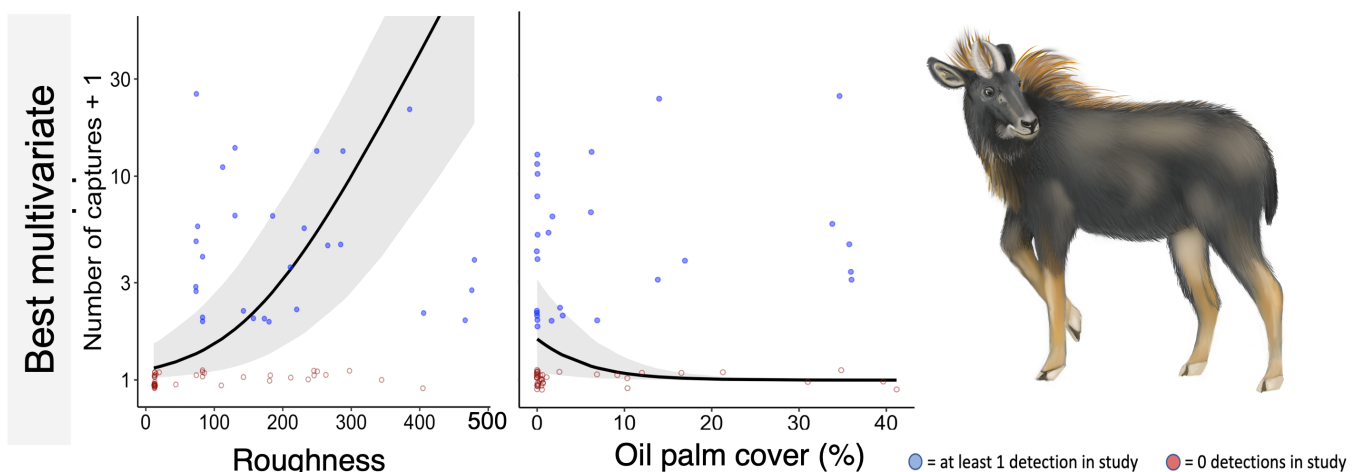
Fig. 4. Regional-scale relationships between serow captures and covariates. Displayed are the variables within the top-performing multivariate model as assessed by lower AICc scores. All covariates are averaged at a 20-km radius around the study area.

SE = ±0.633), a positive effect of roughness (β = 0.447, SE = ±0.200) and a negative effect of Human Footprint (linear, β = -0.559, SE = ±0.323) (Fig. 5). There were other models within 2 AIC scores of the best model. The second-best model differs from the best model by having oil palm cover as a covariate instead of elevation, while the third-best model has oil palm cover and roughness as covariates but not the human footprint index (Table 7).

Table 7. Full list of Royle-Nichols abundance models predicting the local abundance of serow in relation to key habitat variables. All are hierarchal models that account for imperfect detectability and included study landscape as a fixed effect and the effort per sampling cell as a covariate for detection. Only models performing better than the null are shown.

Model	K	AICc	ΔAICc	AICwt	Rsq
oil palm + roughness + Human Footprint Index	15	511.292	0	0.327	0.063
elevation + roughness + Human Footprint Index	16	512.814	1.522	0.153	0.065
oil palm + roughness	14	513.143	1.851	0.129	0.052
oil palm + Human Footprint Index + elevation	15	513.335	2.043	0.118	0.057
oil palm+ Human Footprint Index	14	514.05	2.759	0.082	0.049
oil palm+ roughness + elevation	15	514.197	2.905	0.076	0.055
oil palm + elevation	14	514.884	3.592	0.054	0.047
oil palm	13	517.164	5.872	0.017	0.034
elevation + Human Footprint Index	14	518.352	7.061	0.01	0.037
oil palm+ forest cover	14	518.44	7.148	0.009	0.036
oil palm + forest loss	14	519.021	7.729	0.007	0.035
roughness	13	520.148	8.857	0.004	0.025
elevation	13	520.201	8.909	0.004	0.025
elevation + forest cover	14	520.321	9.029	0.004	0.031
Human Footprint Index	13	521.297	10.005	0.002	0.022
elevation + forest loss	14	521.816	10.525	0.002	0.026
forest cover	13	522.933	11.642	0.001	0.017
degraded forest	13	523.201	11.909	0.001	0.016
forest loss	13	526.384	15.092	0	0.006
Null (~Cell effort ~ session id)	12	526.496	15.204	0	0
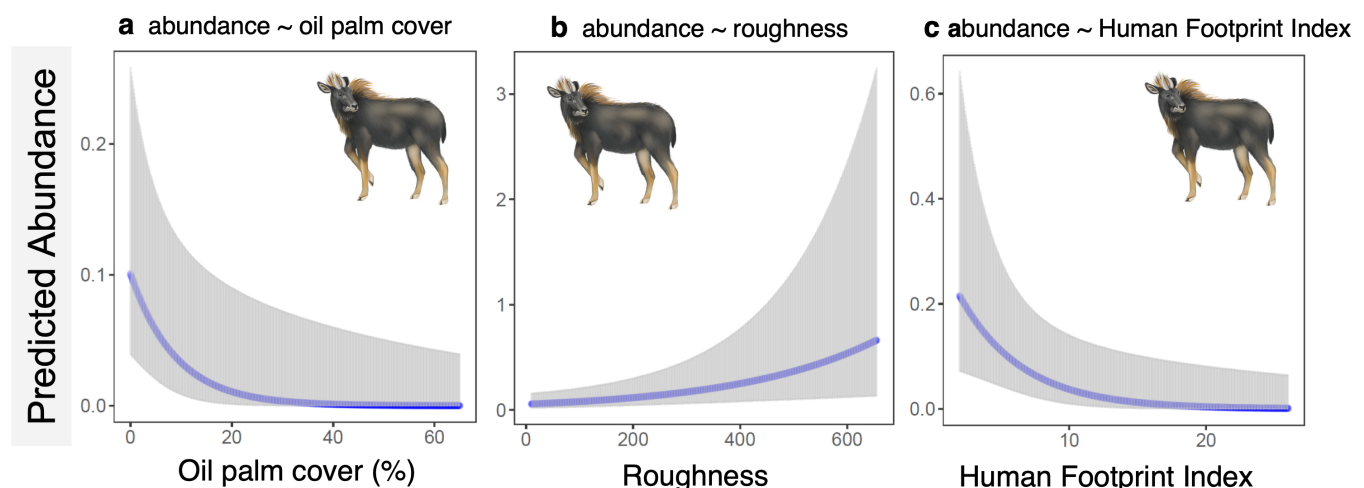
Fig. 5. The relationships between serow predicted abundance and habitat variables at the local scale from Royle-Nichols hierarchical models. Oil palm, roughness and Human Footprint Index were in the top performing multivariate model.

DISCUSSION

Serow were positively associated with landscape roughness and negatively associated with anthropogenic factors (i.e., oil palm landcover and human footprint) across all scales. Interestingly, serow showed consistent responses to habitat variables across multiple-scales, despite it being known that species' distributions can be affected by different scales (Tilker et al., 2020). We also documented a smaller predicted AOO than the current IUCN-identified range (Phan et al., 2020). We note that their strongest association across all spatial scales was avoiding oil palm, whose landcover is predicted to markedly increase with climate change enabling arable conditions to expand upward to mid- and high-elevational zones (Struebig et al., 2015; Brodie, 2016; Zeng et al., 2018). In Nepal, Paudel & Kindlmann (2012) highlighted that serow have been extirpated within this mid-elevational range due to agricultural expansion and hunting. On the bright side, landscape roughness deters logging and agriculture (Edwards et al., 2019), so serow may persist in remaining lower elevation, forested hills that have a rougher topography and are less likely to be converted to agriculture, including karst areas. It has also been suggested that serow preference for steep rocky terrain could be for predator avoidance or refugia from hunting (Aryal, 2008). More directly extractive industries such as logging and limestone quarrying in threatened karst environments present conservation challenges for the serow (Clements et al., 2006; Bakri et al., 2020; Pla-Ard et al., 2021).

The serow's avoidance of oil palm could also be driven by both direct and indirect effects. First, serow are predominantly browsers as opposed to frugivores (Lekagul & McNeely, 1988; Phan et al., 2012) and so oil palm fruits are unlikely to be a direct food resource. Second, given the demand for serow within the wildlife trade, a highly likely explanation is that roads associated with oil palm plantations are indirectly enabling hunting in and around plantations (Luskin et al., 2013). This is corroborated by our results highlighting human footprint as a negative predictor of serow abundance and in other research showing that serow avoid humans (Bhattacharya et al., 2012; Paudel et al., 2015). Phan et al. (2019) and direct observations from the authors (Carr, pers. obs.) found that serow were observed close to ranger stations where hunting was controlled, similarly demonstrating the anthropogenic threats facing serow in unprotected areas.

The serow was identified as one of the top 10 threatened species found for sale within the infamous Golden Triangle in Laos (WWF, 2017). The sale of serow parts also extends online, with it being the second most prevalent species for sale on Facebook surveys within Myanmar (WWF, 2020). The demand for serow is not limited to being 'luxury' restricted for people who can afford it, such as in the case of rhinoceros horn; there is in fact strong demand for serow in the lower socio-economic bracket, with one study demonstrating that serow were the most frequently used wildlife medicine of rural households surveyed in Laos (Johnson et al., 2003). Another worrying trend is that, due to the growing cost of bear bile, serow bile is becoming increasingly sought after

as a cheaper alternative (Davis & Glikman, 2020). Taken together, this evidence suggests the importance of serow for humans and threats posed by hunting may have been underestimated to date.

Just half of the serow's IUCN Red List range remains forested and only 16 % of that forested range is under some form of declared protection. Further, there was a low probability of presence across Sumatra and one of the largest forests of Peninsular Malaysia, the Ulu Muda landscape (Ali, 2014). We also noted several records from outside the recognised Southeast Asia IUCN Red List range, including the Virachey National Park in Cambodia. Recent discoveries of serow in previously unknown areas, such as from Gunung Ledang National Park in Johor, Malaysia, also suggest that serow may persist in isolated lower-elevation parks where poaching is regulated or possibly demonstrate recolonisation events where serow were previously extirpated (Bakri et al., 2020). These occurrence records may moderately expand the known extant range of serow.

Future research and conservation directives. The synergistic threats of deforestation, expanding agriculture, climate change, and high demand in the wildlife trade are impacting Southeast Asian serow. Addressing non-climate change-related threats to wildlife populations helps alleviate pressures and increases their resilience to future threats (Prober et al., 2019). We acknowledge that range-wide occupancy-only distribution studies may be limited due to incomplete sampling, for example in Myanmar and Vietnam. Our findings however offer future research hypotheses, as well as provide policymakers additional considerations when planning for conservation. Little is known about serow diets and behaviour (Phan et al., 2020), including home range size, and breeding and inter-calving periods, which could help further assess the impact of hunting (Foden et al., 2019). The renewed focus towards the impacts of the wildlife trade in the wake of the COVID-19 pandemic has given governments such as Vietnam (Thi et al., 2021) the catalyst for strengthening and enforcing existing wildlife trade laws. Serow conservation will benefit from the reduction of oil palm agricultural expansion, protection of 'rough' landscape habitats, and greater enforcement of illegal hunting.

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AUTHOR CONTRIBUTIONS

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APPENDIX

Appendix 1. Camera trapping studies in published literature used for analysis.

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