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Sumatra-wide assessment of spatiotemporal niche partitioning among small carnivore species

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Abstract
Niche partitioning is a result of interspecific competition between closely-related species to allow co-existence. Multiple species of small carnivores co-occur throughout their ranges in Sumatra, but they are among the lesser studied group of mammal species. This study aimed to collate occurrence records of small carnivores, model their island-wide spatial distribution, and assess their spatio-temporal niche partitioning in Sumatra. We collated camera trap records of small carnivores that were mainly bycatch data from widespread tiger surveys. We used Maxent to predict suitable habitat for nine small carnivore species in response to environmental variables, calculated pairwise spatial niche overlap, and then assessed temporal overlap using Kernel density estimation. In total, we detected 16 of the 21 small carnivore species known to occur in Sumatra. We predicted the suitable habitat of nine species that were found in ≥ 20 locations. Species with the smallest extent of predicted suitable habitat were the Malay civet (*Viverra tangalunga*) and short-tailed mongoose (*Herpestes brachyurus*). Of 36 pairwise comparisons, five species pairs had high overlaps and four species pairs had low overlap on spatiotemporal niche. High overlaps did not necessarily indicate high competition pressure because these species have different behaviour to allow coexistence, such as food preference and arboreality. Camera trap surveys are commonly conducted for species-specific studies, yet they also yield abundant records of non-target species. We therefore encouraged collaboration among institutions working in the same region to use bycatch data to fill the knowledge gaps in the ecology of other lesser known species.

Keywords Camera trapping · Interspecific competition · Maxent · Niche segregation · Spatial distribution modelling · Species coexistence

Introduction

Multiple species which share similar resource undergo interspecific competition when resources are limited, including within carnivorous mammal community (Petersen et al. 2019). Coexisting carnivores may alter their activity patterns (e.g., Lucherini et al. 2009; Gerber et al. 2012; Chutipong et al. 2017) or use different habitats (St-Pierre et al. 2006; Jennings and Veron 2011; Ramesh et al. 2017) to gain access to more resources, resulting in niche partitioning among the coexisting species. However, some studies report that carnivores might also co-occur with substantial spatiotemporal niche overlap, indicating differentiation on other niche dimensions such as behaviour and diet preference (Sunarto et al. 2015; Bu et al. 2016).

More than half of mammal species in the order Carnivora belong to small carnivores; this non-taxon group consists of 153 species in nine families distributed globally on every continent except Antarctica and Australasia (Hunter and Barrett 2011). The ecological features of small carnivores as a group are diverse, comprising ground, aquatic, arboreal, and semi-arboreal species, distributed from marine to freshwater ecosystem and the arid desert to moist tropical forests (Schipper et al. 2008). Sumatra, a part of the Indomalayan realm, is home to 21 small carnivore species, among which one species is endemic to Sumatra, i.e. Sumatran hog badger

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(*Arctonyx hoevenii*). Sumatra is one of the seven core areas identified for small carnivore conservation (Schreiber et al. 1989).

According to the IUCN Red List of Threatened Species (iucnredlist.org), two small carnivore species in Sumatra are listed as Endangered, three as Near Threatened, four as Vulnerable, and as 12 Least Concern. Across their range in Sumatra, each species coexists with one or more other species of small carnivores. McCarthy and Fuller (2014) recorded six small carnivore species in Bukit Barisan Selatan National Park (NP), southern Sumatra; Holden (2006) reported 14 species in Kerinci Seblat NP, central Sumatra (Holden 2006); in an oil palm plantation, Jennings et al. (2011) found three small carnivore species.

Regardless of the diversity of small carnivores in Sumatra, little is known about their distribution, ecology, and threats as most of the research and conservation effort in this region is more focused on charismatic megafauna, in particular the Sumatran tiger *Panthera tigris sumatrae* (Linkie et al. 2008; Wibisono et al. 2011). Habitat loss is one of the main causes of population declines for small carnivores because most of them are vulnerable to human-modified landscapes (Schipper et al. 2008). In Sumatra, 35.7% of primary forests were lost between 1990 and 2010, and the remaining primary forest cover was only 30% of the land area in 2010 (22% primary degraded forest and 8% primary intact forest) (Margono et al. 2012). Many small carnivore species, however, can thrive in a logged forest (Mathai et al. 2010) and plantations (Jennings et al. 2015) due to high abundance of rodents and other prey. Wildlife trading potentially threatens small carnivore populations. There are only a few reports on small carnivores trading in Sumatra (Shepherd 2008, 2012) and the impact of the trading on wild population of small carnivores remains unknown. Only eight of the 24 small carnivores in Indonesia (3 non-Sumatran species) are listed as protected species under Indonesian law (Ministerial Regulation No. 106 Year 2018 concerning the Updated Protected Species List), and the law enforcement for trading permits and harvest quotas is weak (Shepherd 2008, 2012). Aquatic and semi-aquatic small carnivores are susceptible to the contamination of water bodies (Schipper et al. 2008; Hussain et al. 2011). Habitat loss and unmeasured threats, such as those from wildlife markets, may lead to 'silent extinctions'. Therefore, it is important to study the status and distribution of small carnivores as the baseline knowledge for conservation management.

In Sumatra, extensive camera trap surveys have been conducted for a few mammal species, such as tiger (O'Brien et al. 2003; Linkie et al. 2006; Pusparini et al. 2018), Sunda clouded leopard (*Neofelis diardi*) (Haidir et al. 2018) and sun bear (*Helarctos malayanus*) (Wong et al. 2012), yet there was also a considerable number of by-catch records of other species. These bycatch records have been used to assess ecological features of less known species, such as small carnivores (Holden 2006; Cheyne et al. 2010; Pollock et al. 2015) and cats (Pusparini et al. 2014; Sunarto et al. 2015). However, the extents of these studies in Indonesia were usually at a local scale (site-specific). While there have been a number of large-scale studies on Bornean small carnivores (e.g., Kramer-Schadt et al. 2016; Ross et al. 2017; Hearn et al. 2018), little is known about the distribution and how the coexisting small carnivore species segregate niche across space and time in Sumatra. Considering these gaps, we aimed to (i) collate occurrence records of small carnivores from multiple camera trap projects in Sumatra; (ii) predict the spatial distribution patterns of small carnivores; and (iii) assess spatiotemporal niche partitioning among small carnivores in Sumatra.

Methods

Study region

Sumatra is a part of the Sundaland region, which is regarded as one of the global biodiversity hotspots (Myers et al. 2000). The remarkable feature of the island is the distinctive mountainous Bukit Barisan Range that spans the western half of the island, in contrast with the vast plains in the eastern side (Fig. 1). Elevation ranges from sea level to 3,805 m (the peak of Mount Kerinci). The rainfall regions are divided into two: region A in southern part of Sumatra and region B in northern Sumatra. Region A has one high rainfall peak in January and is strongly influenced by wet northwest monsoon in November-March and the dry southeast monsoon in May–September. Region B has two high rainfall peaks in October–November and March–May which are associated with the movement of the inter-tropical convergence zone (Aldrian et al. 2003). Laumonier (1997) divided the bioclimates into the following five categories based on the annual rainfall: subhumid with an annual rainfall of 1000–1500 mm in 1% of Sumatra, humid (1500–2000 mm) in 4.3%, very humid (2000–2500 mm) in 30, superhumid (2500–3000 mm) in 29%, and hyperhumid (> 3000 mm) in 35.7%.

Species occurrence records

We collated small carnivore records from 13 camera trap projects, comprising nine sites/landscapes, conducted by individual researchers and non-profit organisations in collaboration with governmental institutions or private industries across Sumatra (Fig. 1, Table 1). Most of the surveys targeted tigers, except a dataset in Bukit Barisan Selatan NP which targeted terrestrial vertebrates, WMW in Kerinci-Seblat NP for sun bear, and IDS in Southern Solok for small cats. We discarded

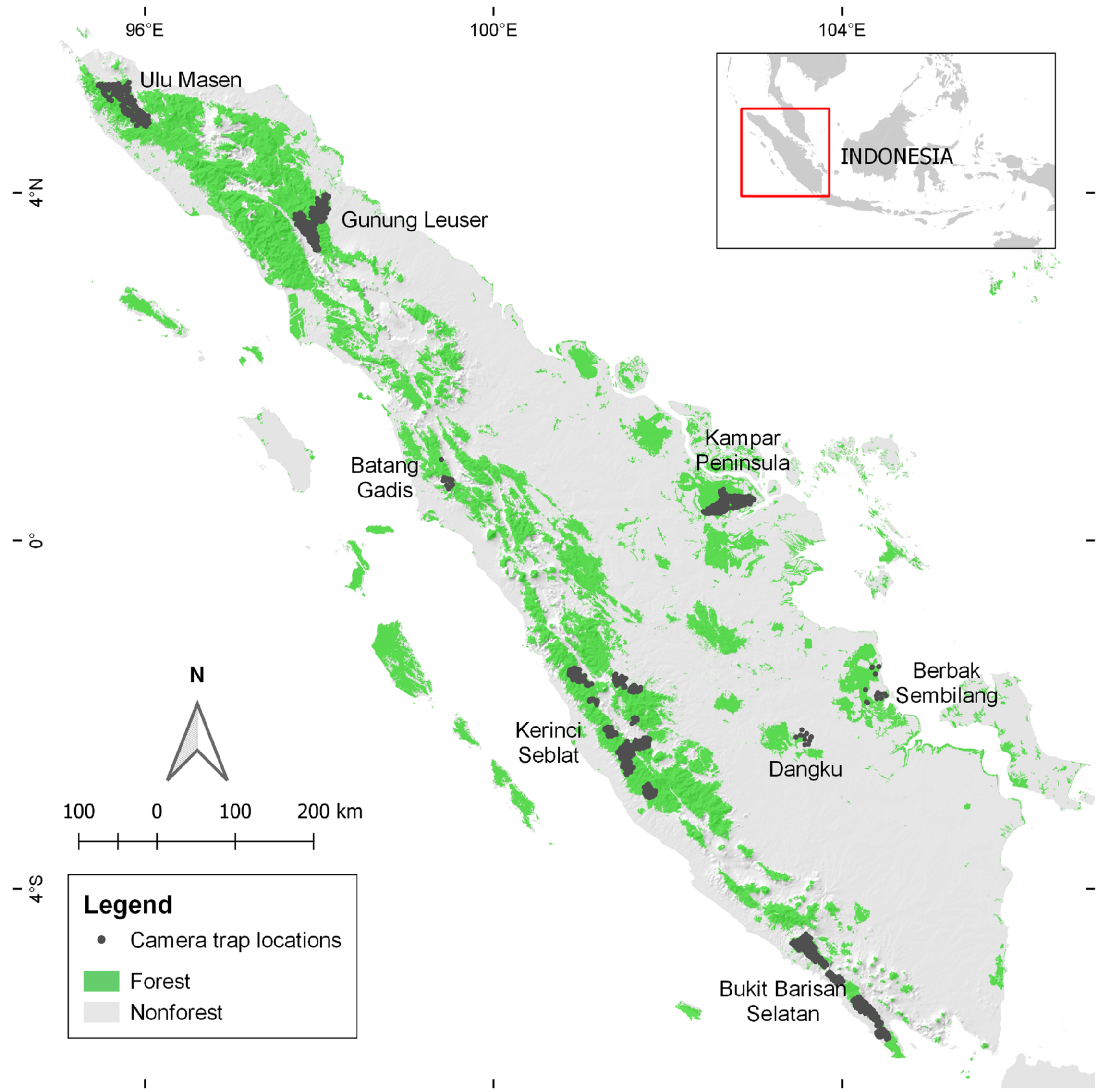

Fig. 1 Camera trap survey locations across Sumatra. Most camera trap locations were in forested area (80.2% dryland forest, 13.7% swamp forest, 2.6% agriculture, 2.8% bush-bareland, 0.4% mangrove forest, 0.3% open area)

camera trap records of small carnivores with uncertain species identification and missing time and location information. Of a total 3809 records in the original spreadsheets, we could collect and verify 90.5% of photographs. Of these, we found that there were three empty photos, one unknown small carnivore, and six non-small carnivores photos which were removed. These photographs were then re-verified by Dr. William Duckworth, a small carnivore expert, to ensure reliable species identification.

Predictive spatial distribution modelling of small carnivore species

We used Maxent to create predictive distribution maps of small carnivore species which were detected in at least 20 different camera trap locations. Maxent takes species presences and a set of environmental variables across a geographical space to predict a species's environmental suitability. The output of Maxent modelling is a raster maps

Table 1 Datasets of small carnivore occurrence records and the details of corresponding camera trap surveys

Site	Main target	Survey period	Mean (SD) distance between nearest camera traps (m)	Number of camera trap locations	Survey effort (trap-nights)	Surveyed elevation range (m)	Data source
Ulu Masen PF	Tiger	2012–2013	1769 (766)	151	6504	210–1771	FFI
Gunung Leuser NP	Tiger	2010	2135 (1147)	69	3356	44–2927	GLNP, WCS, Panthera
Gunung Leuser NP	Tiger	2013	1846 (641)	116	5573	106–2996	GLNP, WCS, Panthera
Batang Gadis NP	Tiger	2005–2006	2181 (1372)	16	539	621–1512	BGNP, CI
Restorasi Ekosistem Riau (RER) Concessions, Kampar Peninsula	Tiger	2015	1692 (702)	138	7431	9–33	FFI, RER[1]
Kerinci-Seblat NP	Tiger	2012–2015	1447 (884)	188	9561	273–2273	KSNP, FFI, Panthera
Kerinci-Seblat NP	Sun bears	2009–2011	1921 (410)	126	8813	145–1968	KSNP, WM Wong[2]
Solok Selatan, Kerinci-Seblat Landscape	All animals	2015–2018	652 (458)	38	6748	419–1023	ID Solina, Tidar Kerinci Agung Company[3]
Berbak Sembilang NP	Tiger	2015–2016	4684 (3999)	15	1791	6–937	BSNP, ZSL
Dangku WR	Tiger	2016	5387 (2555)	15	710	23–937	South Sumatra NCA, ZSL
Bukit Barisan Selatan NP	Terrestrial vertebrate	2010–2015	1385 (24.3)	60	8561	16–320	BBSNP, WCS[4]
Bukit Barisan Selatan NP	Tiger	2015	2052 (487)	65	9037	164–936	BBSNP, WCS, Panthera[5]
Bukit Barisan Selatan NP	Tiger	2018	3766 (479)	61	6826		BBSNP, WCS

Sites were sorted from the northernmost to southernmost of Sumatra

NCA Nature Conservation Agency, *NP* National Park, *NR* Nature Reserve, *PF* Protection Forest, *WR* Wildlife Reserve. References for camera trap survey methods: [1]Avriandy et al. (2016), [2]Wong and Linkie (2013), [3]Solina et al. (2018), [4]TEAM Network (2011), [5]Pusparini et al. (2018)

All cameras were set up without baits

containing a relative index of predicted environmental suitability, where higher values represent a better predicted condition for the species (Phillips et al. 2006). To reduce the effects of spatial autocorrelation, we only used species records that were separated at least 1 km.

We considered eight habitat covariates in the Maxent modelling: elevation, slope, roughness, tree cover, land cover, distance to human-modified habitat, human population density, and annual precipitation. We obtained elevations from SRTM digital elevation model v4.1 at 90 m resolution (Jarvis et al. 2008) and derived slopes and roughness data from the elevation model. We used global tree canopy cover circa 2010 at a 30-m spatial resolution of Hansen et al. (2013) to represent tree cover percentage. We extracted land cover information using a land cover map of Sumatra (MoEF, 2016). The data consisted of 22 land-use types, for which we then combined similar land uses and excluded water bodies, resulting in six main land-use types; agriculture, bush/bareland, dryland forest, mangrove forest, savannah, and swamp forest. Although the species occurrence data ranged between 2005 and 2018 and we used tree canopy cover and land cover data from only one year, most of the camera trap locations were in protected areas where tree cover is less likely to degrade or lose compared to non-protected areas. Margono et al. (2012) reported that protected areas only accounted for 9% of total forest cover loss in 1990–2010, compared to 65.8% in production forests. Distance to human-modified habitat—agriculture, settlement, and infrastructures of MoEF (2016) land use map—were measured as Euclidean distance from the periphery of modified habitat polygons to grid cells at non-modified habitat (primary forest and secondary forest). This process resulted in all human-modified land uses having a value of 0 m and the highest value occurring in the middle of a large patch of forest. We used a gridded map of the estimated total number of people per grid-cell at 100 m resolution (WorldPop 2014) to represent human population density. We used average monthly rainfall data at 1 km resolution from WorldClim 2.1 (Fick and Hijmans 2017), and summed them to obtain the annual rainfall data. All raster data were resampled into a resolution of 1 km, i.e., the coarsest resolution of the original raster data, and vector variables were rasterized into a gridded map at the same resolution. We tested for collinearity among variables and removed variables with Pearson's $|r| > 0.75$ (Kramer-Schadt et al. 2013). As a result, we excluded the roughness and slope (Supporting Information, Table S1). We conducted all spatial data processing and statistical computing using the R programming language version 3.5.2 (R Core Team 2018).

We modelled species distribution using Maxent version 3.4.1 (Phillips et al. 2017). To reduce model overfit, we only used linear, quadratic, and product features for the predictors (Merow et al. 2013). Using simpler features had been suggested to reduce random noise from general species responses to the environment (Syfert et al. 2013). We used tenfold cross-validation to evaluate model predictions for each species. All other model settings remained default (regularization multiplier = 1; maximum number of background points = 10,000). Although our camera trap stations were distributed across Sumatra, they were clustered in only a few sites, mostly in forested areas (Fig. 1). Therefore, we created a sampling bias file by mapping camera trap locations on a 300-m gridded map and assigning a value of 1 on cells within 1 km radius from the camera trap locations. Other cells were given a value of 0.1, following Kramer-Schadt et al. (2013). The result of this background manipulation was that instead of generating background points evenly across Sumatra, Maxent generated more background points around locations where camera traps were placed, and hence approximating the true sampling effort.

Although from camera trap surveys we could obtain detection/non-detection data, our non-detection might occur due to low detection probability instead of true absences. Therefore, we could not use logistic regression, which requires presence/absence data, to predict species distribution. Occupancy modelling allows estimating detection probability from repeated sampling with population closure assumption (Linkie et al. 2007). However, given the differences in survey periods and survey methods (Table 1), our dataset did not meet the closed population assumption and was therefore not suitable for occupancy analysis.

Estimating spatial distribution overlap

To calculate pairwise spatial overlap, we used the function 'calc.niche.overlap' of the R package 'ENMeval' (Muscarella et al. 2014). The function takes two species predicted distribution maps as inputs and calculates the Schoener's *D* overlap index based on the habitat suitability value on each grid cells. This overlap index was regarded as a good index to calculate niche overlap based on predictive spatial distribution maps (Rödder and Engler 2011). The index ranged between 0, indicating no overlap, and 1, indicating complete overlap.

Estimating diel activity pattern overlap

At each location, species detections more than 30 min apart were considered to be independent and were used to assess the diel activity patterns of each species (O'Brien et al. 2003; Ridout and Linkie 2009). To estimate the activity pattern overlap, we followed the method developed by Ridout and Linkie (2009) and Linkie and Ridout (2011). Time of species activity recorded by camera trap was treated as circular data ranging from 0 to 2π radians. The coefficient of overlap of species pairs is calculated non-parametrically using Kernel density estimation (Ridout and Linkie 2009). For species pair with less than 75 records each, we chose Δ_1 as the overlap measure. Otherwise, Δ_4 is calculated. Overlap calculations were conducted using the R package 'overlap' (Meredith and Ridout 2014). We used arbitrary cut-off values of > 0.6 for high overlaps and < 0.4 for low overlaps, and categorised values in between as medium overlaps to ease presenting results.

Results

From a total of 75,450 trap nights recorded at 1,058 camera trap locations, we found 16 small carnivore species representing five families (Table 2). Species that are known to occur in Sumatra, yet not recorded in our study, were Javan mongoose (*Herpestes javanicus*), Eurasian otter (*Lutra lutra*), hairy-nosed otter (*Lutra sumatrana*), smooth-coated otter (*Lutrogale perspicillata*), and Malay weasel (*Mustela nudipes*). Species that were frequently recorded and widely distributed across surveyed sites included yellow-throated marten (*Martes flavigula*), banded linsang (*Prionodon linsang*), banded civet (*Hemigalus derbyanus*), masked palm civet (*Paguma larvata*), and binturong (*Arctictis binturong*). Short-tailed mongoose (*Herpestes brachyurus*) and Malay civet (*Viverra tangalunga*) were also frequently recorded, but most of the locations where the two species were recorded (92% and 94%, respectively) were from one site only, i.e. Kampar Peninsula in Central Sumatra.

Predictive distribution models of small carnivore species in Sumatra

The area under the receiver operating characteristic curve (AUC) values of all Maxent models for the nine species was above 0.7, indicating a good model fit to the training data

Table 2 Number of species detections at each study site

Species names	Common names	Red List status	Number of unique camera trap locations with species detections								
			Ulu Masen (151)	Gunung Leuser (185)	Batang Gadis (16)	Kampar Peninsula (138)	Kerinci Seblat (352)	Dangku (15)	Berbak Sembilang (15)	Bukit Barisan Selatan (186)	Total
Herpestidae											
*Herpestes brachyurus**	Short-tailed Mongoose	NT	–	–	–	54	–	1	3	1	59
Herpestes javanicus	Javan Mongoose	LC	–	–	–	–	–	–	–	–	–
Herpestes semitorquatus	Collared Mongoose	NT	–	1	–	–	–	–	–	1	2
Mephitidae											
Mydaus javanensis	Sunda Stink Badger	LC	–	–	–	–	1	–	–	11	12
Mustelidae											
Aonyx cinereus	Asian Small-clawed Otter	VU	–	–	–	–	1	–	2	2	5
*Arctonyx hoevenii**	Sumatran Hog Badger	LC	14	10	–	–	16	–	–	5	45
Lutra lutra	Eurasian Otter	NT	–	–	–	–	–	–	–	–	–
Lutra sumatrana	Hairy-nosed Otter	EN	–	–	–	–	–	–	–	–	–
Lutrogale perspicillata	Smooth-coated Otter	VU	–	–	–	–	–	–	–	–	–
*Martes flavigula**	Yellow-throated Marten	LC	15	48	4	38	44	1	2	27	179
Mustela lutreolina	Indonesian Mountain Weasel	LC	–	1	–	–	–	–	–	–	1
Mustela nudipes	Malay Weasel	LC	–	–	–	–	–	–	–	–	–
Prionodontidae											
*Prionodon linsang**	Banded Linsang	LC	9	32	3	4	31	–	1	14	94
Viverridae											
*Arctictis binturong**	Binturong	VU	13	4	1	6	13	–	2	15	54
Arctogalidia trivirgata	Small-toothed Palm Civet	LC	–	–	–	4	1	–	–	1	6
Cynogale bennettii	Sunda Otter Civet	EN	–	–	–	–	–	–	1	1	2
*Hemigalus derbyanus**	Banded Civet	NT	21	23	–	49	1	1	5	38	138
*Paguma larvata**	Masked Palm Civet	LC	35	53	10	–	86	–	–	47	231
*Paradoxurus hermaphroditus**	Common Palm Civet	LC	1	–	–	10	5	7	6	1	30
*Viverra tangalunga**	Malay Civet	LC	–	–	–	83	–	5	–	–	88
Viverricula indica	Small Indian Civet	LC	1	–	–	–	–	–	–	–	1

The numbers in brackets under site names indicate the total number of camera trap locations at corresponding sites

*Species included in spatial distribution modelling and spatiotemporal overlap estimation

Table 3 The area under the receiver operating characteristic curve (AUC) and the contribution of environmental layers to the Maxent models of nine small carnivore species

Species	Training AUC	Percent contribution of environmental layers					
		Land cover	Tree cover	Elevation	Distance to modified habitat	Human population	Annual precipi-tation
Viverridae							
Paguma larvata	0.934	74.5	8.3	9.9	1.9	0	5.4
Paradoxurus hermaphroditus	0.897	78.8	9.9	5	1.2	3.3	1.8
Arctictis binturong	0.901	42.1	53.5	1.9	0.1	0.1	2.3
Hemigalus derbyanus	0.943	22	59.8	5.2	8.6	0	4.3
Viverra tangalunga	0.977	91.1	3.6	1.1	2.3	0.1	1.8
Herpestidae							
Herpestes brachyurus	0.985	87.3	6.3	1.4	3.5	0	1.4
Prionodontidae							
Prionodon linsang	0.926	72.2	18.8	5.1	1.4	0.1	2.4
Mustelidae							
Martes flavigula	0.935	54.3	35	5.5	3.3	0.1	1.9
Arctonyx hoevenii	0.971	61.1	13.1	17.4	1.1	0.1	7.2

Response curves of environmental variables are provided in supporting information, Appendix S4

(Table 3). Malay civet and short-tailed mongoose had the smallest extent of predicted suitable habitat and were limited to peat swamp forests (Fig. 2). Predicted suitable habitat of common palm civet (*Paradoxurus hermaphroditus*) mostly covered lowland areas, but was not in highland forests. In contrast, the Sumatran hog badger (*Arctonyx hoevenii*) seemed to be a highland specialist, with most predicted suitable areas covered highland forests and all occurrence records were above 800 m (Supporting Information, Appendix S3). The extents of predicted suitable habitat for the other five small carnivores were mostly in the forested area of Sumatra which dominantly remained in the western part although this pattern may also reflect the sampling efforts which were mostly in forested area.

Diel activity patterns

Of the nine species assessed for activity pattern, five were nocturnal species (banded linsang, banded civet, masked palm civet, common palm civet, and Malay civet). Diurnal species included short-tailed mongoose, Sumatran hog badger, and yellow-throated marten. There was no preference on time of day shown by binturong (*Arctictis binturong*), indicating cathemeral activity pattern (Fig. 3).

Spatio-temporal niche overlaps

Five species pairs showed high spatio-temporal niche overlaps, while there were four species pairs with low overlaps on both spatial and temporal niche (Fig. 4). However, we also found species pairs with high overlaps on spatial niche, but low temporal overlaps (e.g. between Malay civet and short-tailed mongoose) or vice versa (e.g. between masked palm civet and Malay civet).

Discussion

Our study provides the first island-wide ecological assessment of small carnivores in Sumatra based on a range of camera trap surveys. Other than revealing patterns of niche overlap and partitioning across time and space among small carnivores in Sumatra, our collation of camera trap photographs provided updates on some small carnivore species ranges, some of which have been published elsewhere: Indonesian mountain weasel (*Mustela lutreolina*) in Gunung Leuser NP, which was the first camera trap record for this species (Pusparini and Sibarani 2014) and the first camera trap documentation of a hypopigmented Asian small-clawed otter (*Aonyx cinereus*) in Bukit Barisan Selatan NP (Allen et al. 2019). Previous records of collared mongoose in Sumatra were only from low elevations ≤ 300 m (Holden and Meijaard 2012), but a survey in Gunung Leuser NP recorded this species at a higher altitude of 666 m in July 2013 (Pusparini and Sibarani 2014) and another survey in Bukit Barisan Selatan NP recorded it at 436 m in August 2015 at 7:04 AM (Fig. 5). Small Indian civet (*Viverricula indica*) is widely distributed in mainland Asia and extends to Java, but its extent of occurrence in Sumatra is still

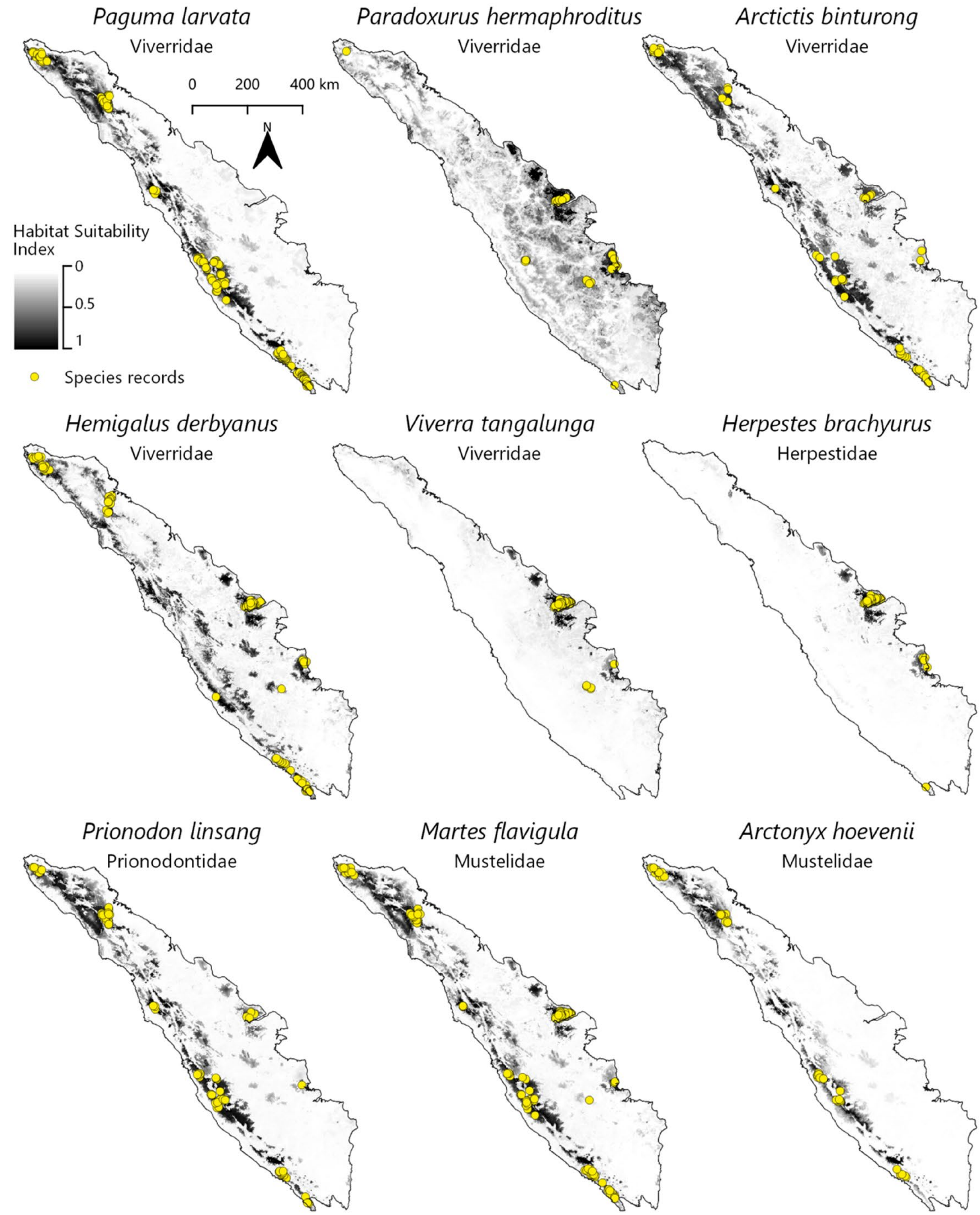

Fig. 2 Predicted distribution maps of nine small carnivore species across Sumatra

unclear (Choudhury et al. 2015). We found one record of small Indian civet (Fig. 5) in its known range in Sumatra, that is in Ulu Masen, at 288 m in a dryland agricultural area, consisting of four occasions between January and February 2013. We recorded a Sunda otter civet (*Cynogale bennettii*), an Endangered small carnivore species, in a lowland dryland forest at 86 m altitude in 2011 and in a mangrove forest at 19 m in 2015, further confirming its habitat use in lowland forest (Ross et al. 2015).

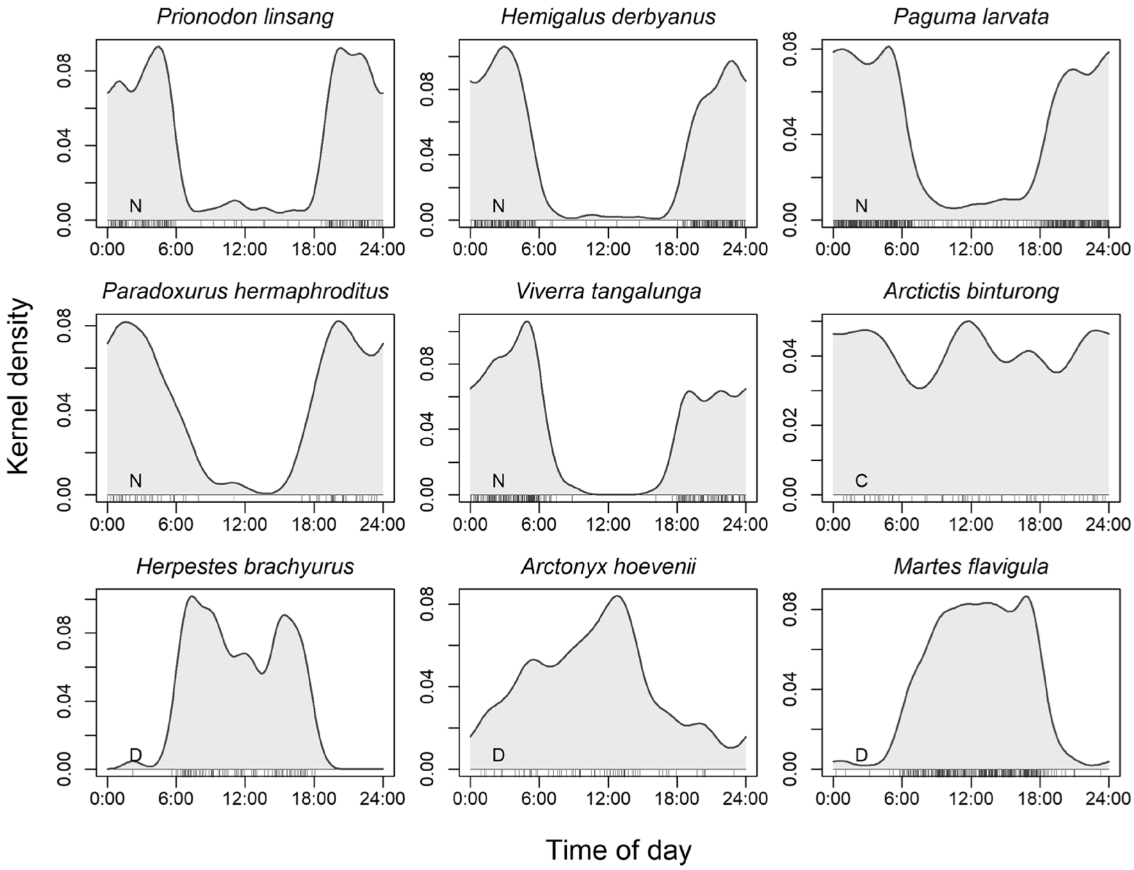

Fig. 3 Kernel density distribution of activity patterns of nine small carnivores found at > 20 locations. The rugs at the bottom of the density curves show the time of the day at which the species were photographed. Graphs were sorted based on species' diel activity patterns: *N* nocturnal, *D* diurnal, and *C* cathemeral

Habitat specialists

Of the nine species modelled for their suitable habitat, we found three species that were predicted to have restricted habitat use: Malay civet, short-tailed mongoose, and Sumatran hog badger. Malay civet and short-tailed mongoose showed a predicted preference for lowland swamp forests in eastern Sumatra and there were only a few records in dryland forests. Previous studies suggest that they are indeed lowland specialists (Jennings and Veron 2011; Duckworth et al. 2016a, b; Ross et al. 2016; Solina et al. 2018). The predictive distribution models by Jennings and Veron (2011) found that evergreen forest is highly suitable habitat for short-tailed mongoose and Malay civet in Southeast Asia. None of the georeferenced occurrence records of the short-tailed mongoose and Malay civet used by Jennings and Veron (2011) was from swamp forests, whereas 95% of short-tailed mongoose and 92% of Malay civet occurrences in our study were from swamp forests. As a result, their resulting prediction maps were markedly differed from those of ours. These contrasting results suggested that species' predicted suitable habitat might be different when modelled on different scale and that researchers should be cautious when drawing inferences from incomplete data sets. The species occurrence data from our study came from comparable trapping efforts between lowland (< 150 m) dryland and swamp forests (46% trap-nights in dryland forest vs. 40% in swamp forest; 32% camera trap locations in dryland forest vs. 55% in swamp forest), so it might be possible that the Malay civet and short-tailed mongoose in Sumatra preferred lowland swamp forests over dryland forests.

Another habitat specialist small carnivore is the Sumatran hog badger, which was always recorded at higher elevations (> 800 m) in our study. This finding is consistent with the habitat description by Helgen et al. (2008), who suggested that this species occurs in low montane forests to subalpine meadows.

Coexistence mechanisms for small carnivores

The competitive exclusion principle suggests that two species may coexist if they differ on at least one niche

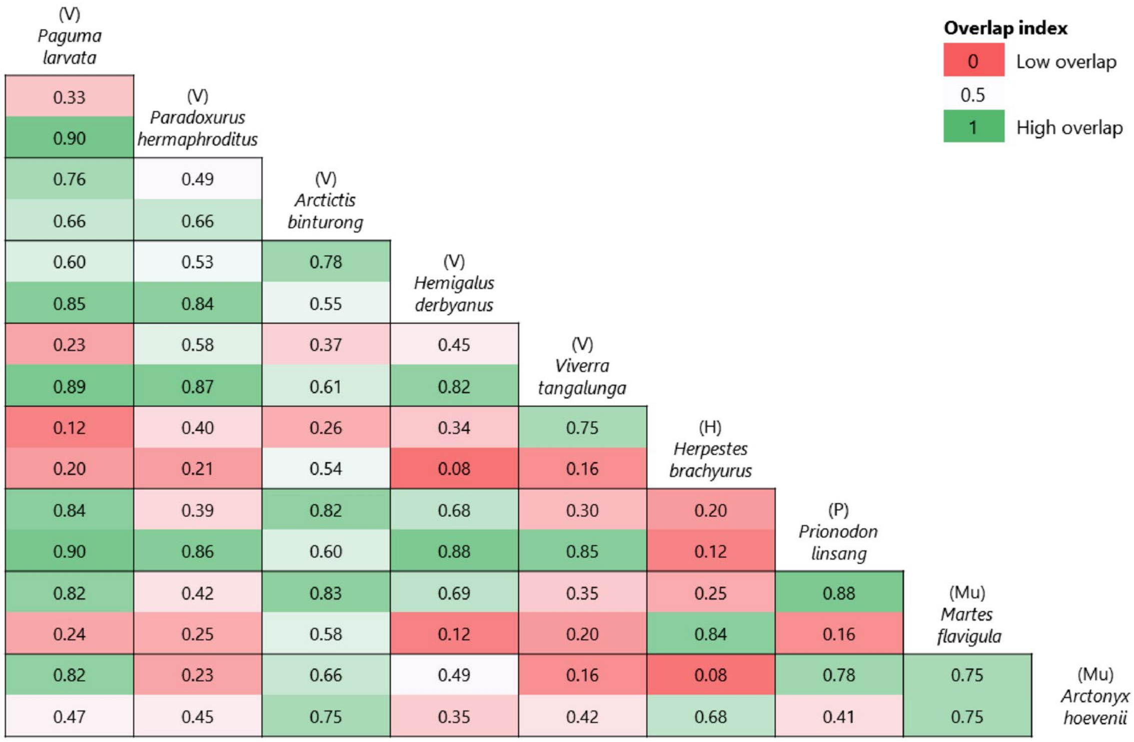

Fig. 4 Species-pair overlap matrix. The numbers on the upper half in the species-pair cells are spatial overlap indices between corresponding species; the numbers on the lower half are temporal overlap indices. Darker shades of green represent higher overlap; darker shades of red represent lower overlap. Letters in brackets represent family (*V* Viverridae, *H* Herpestidae, *P* Prionodontidae, *Mu* Mustelidae, *Me* Mephitidae)

dimension (Hardin 1960). Our findings showed species pairs that had high overlap on one niche dimension and high segregation on another dimension. Malay civet and short-tailed mongoose are two common species in Kampar. Both were mostly found in lowland swamp forests in Sumatra and therefore had high spatial overlap. However, there is almost complete segregation on the temporal niche between the two: the Malay civet is nocturnal, whereas the short-tailed mongoose is mostly active during the day, as found in previous studies (Colón 2002; Jennings et al. 2010; Jennings and Veron 2011).

Species with high niche overlaps on both spatial and diel activity pattern do not necessarily suffer from competition pressure. They may perform segregation on other niche dimensions not assessed in this study, especially their feeding habit. For example, two sympatric mustelid species, yellow-throated marten and Sumatran hog badger, had high niche overlap in their spatial distribution and their activity pattern. However, the yellow-throated marten, a semi-terrestrial species, is generally known as predator of small vertebrates and occasionally feeding on plant matter (Parr and Duckworth 2007), whereas the Sumatran hog badger is strictly terrestrial and feeds on soil invertebrates, such as earthworms, beetle larvae, and ants, and occasionally non-invertebrates (Helgen et al. 2008).

Study limitations

This study employed camera trap records that mostly came from large mammal surveys. Camera trap installation was done in a way that optimises capture probability for the target species. Therefore, the data may underestimate or overestimate the occurrence of non-target species. First, some small carnivore species in Sumatra are semi-terrestrial and arboreal species which often or rarely come to the ground (Hunter and Barrett 2011); consequently, these species were underrepresented in this study. Second, we only found few records of semi-aquatic species, such as the Sunda otter civet, because most of camera trap stations were not placed close to water bodies. Three of the five non-recorded species, i.e., Eurasian otter (*Lutra lutra*), hairy-nosed otter (*Lutra sumatrana*), and smooth-coated otter (*Lutrogale perspicillata*), are highly water-associated and are hardly recorded in general camera trapping. Another caveat of this study is that sampling effort was biased toward dryland forests (81% of the camera stations); thus the results may underrepresent

Fig. 5 Camera trap photographs of a collared mongoose **a** in Bukit Barisan Selatan National Park (© BBTNBBS, WCS, Panthera), a small Indian civet **b** in Ulu Masen Protection Forest (© BKSDA Aceh, FFI), and a Sunda otter covet **c** in Bukit Barisan Selatan National Park (© BBTNBBS, WCS, TEAM Network)

species that prefer non-forest habitat or habitat generalists that are little affected or positively affected by habitat modification and disturbance, such as Javan mongoose, common palm civet, and small Indian civet. Camera traps were usually set up at a relatively high height, 45–50 cm above ground, which may be too high for small carnivores, resulting in missed detection. The datasets we have collated are the most extensive available data for Sumatran small carnivores, but we note that it is unlikely to detect all species present during a survey.

Conclusion and suggestions for future studies

Small carnivores are among the lesser studied mammals, and there is limited research and conservation funding targeting small carnivores compared to their larger cousin carnivores which are often regarded as umbrella and flagship species. Research efforts for cat species were known to be biased towards larger animals regardless of their threat status (Brodie 2009). Bycatch records of non-target species are useful to infer the distribution and ecology of less known species although it also comes with shortcomings. We, therefore, encourage other researchers and conservation practitioners to collate occurrence data of the other non-target, yet threatened species in Sumatra, such as non-*Panthera* cats, sun bear, dhole (*Cuon alpinus*), Sunda pangolin (*Manis javanica*), Sumatran ground cuckoo (*Carpococcyx viridis*), crested partridge (*Rollulus rouloul*), black partridge (*Melanoperdix niger*), Malay crestless fireback (*Lophura erythrophthalma*), Malay crested fireback (*Lophura rufa*), bronze-tailed peacock-pheasant (*Polyplectron chalcurum*), and great argus (*Argusianus argus*), as well as data deficient species, such as Sumatran striped rabbit (*Nesolagus netscheri*) and Sumatran mountain muntjac (*Muntiacus montanus*). Species population are declining due to increasing extinction threats; therefore, having a better understanding of their current occurrence and environmental factors affecting them using the best available data is important for their conservation and habitat management. Finally, collaborative research and responsible data-sharing among institutions which conducts camera traps surveys are also crucial to establish a complete regional-scale comparative study.

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Author contributions MS, WP: conceptualization; All authors: methodology; WRA, AA, TA, RA, YD, TK, DK, BN, WN, Radinal, DS, AS, Sismanto, IDS, RAS, MVW, W-MW: Data curation; MS, WP: Formal analysis and investigation; MS: Writing—original draft preparation; All authors: Writing—review and editing; WP: Supervision.

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Data availability All data generated or analysed during this study are included in this published article and its supplementary information files.

Code availability Not applicable.

Declarations

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