

1 **Carnivore hotspots in Peninsular Malaysia and their** 2 **landscape attributes**

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34 ~~*deliberative and pre-decisional, so it must not be disclosed or released by reviewers. Because the*~~
35 ~~*manuscript has not yet been approved for publication by the U.S. Geological Survey (USGS), it does not*~~
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37 **Abstract**

38 Mammalian carnivores play a vital role in ecosystem functioning. However, they are prone to
39 extinction because of low population densities and growth rates, [large area requirements](#), and
40 high levels of persecution [or exploitation](#). In tropical biodiversity hotspots such as Peninsular
41 Malaysia, rapid conversion of natural habitats threatens the persistence of this vulnerable
42 group of animals. Here, we carried out the first comprehensive literature review on 31
43 carnivore species reported to occur in Peninsular Malaysia and updated their probable
44 distribution. We georeferenced 375 observations of 28 species of carnivore from 89 unique
45 geographic locations using records spanning 1948 to 2014. Using the Getis-Ord G_i^* statistic and
46 weighted survey records by IUCN Red List status, we identified hotspots of species that were of
47 conservation concern and built regression models to identify environmental and anthropogenic
48 landscape factors associated with Getis-Ord G_i^* scores. Our analyses identified two carnivore
49 hotspots that were spatially concordant with two of the peninsula's largest and most
50 contiguous forest complexes, associated with Taman Negara National Park and Royal Belum
51 State Park. A cold spot overlapped with the southwestern region of the Peninsula, reflecting the
52 disappearance of carnivores with higher conservation rankings from increasingly fragmented
53 natural habitats. Getis-Ord G_i^* scores were negatively associated with elevation, and positively
54 associated with the proportion of natural land cover and distance from the capital city.
55 Malaysia contains some of the world's most diverse carnivore assemblages, but recent rates of
56 forest loss are some of the highest in the world. Concerted efforts to reduce poaching and
57 maintain large contiguous tracts of lowland forests will be critical, not only for the persistence
58 of large mammals, but for threatened carnivores in general.

59 **Key words:** predator, tropical rainforest, landscape, hotspot, coldspot, Carnivora

60 **Introduction**

61 Few taxonomic groups elicit as much conservation attention as mammalian carnivores [1-3].
62 Carnivores of various sizes play a crucial role influencing the composition and dynamics of
63 ecological communities [4]. The loss of apex predators has been linked to cascading
64 consequences for smaller herbivores regulated by mid-order predators [5-6], which in turn can
65 influence plant growth and recruitment via altered patterns of herbivory, seed predation, and
66 seed dispersal [3,4,7,8]. Charismatic carnivores often serve as conservation flagships [9], and
67 when their area and resource requirements encompass those of numerous species, they serve
68 as conservation umbrellas [10-12]. Carnivore presence may be linked positively with
69 biodiversity [13,14] habitat integrity [15] and ecological processes [4]. Ironically, the very
70 characteristics that make carnivores such effective conservation surrogates also make them
71 extinction-prone.

72 Mammalian carnivores are vulnerable to extinction mainly due to habitat loss and human-
73 induced mortality [16,17]. Carnivores in general occupy the higher region of ecological food
74 webs, composing a relatively small fraction of ecological biomass and requiring a healthy prey

75 base to maintain viable populations. Large carnivores need substantial areas that support the
 76 prey they subsist on and some level of functional landscape connectivity for persistence. Loss of
 77 habitat and prey renders them prone to conflicts with humans [18–21]. Furthermore, carnivores
 78 are prime targets for poachers seeking valuable body parts or trophies [22–25] and their life
 79 histories often hinder recovery from population declines [26]. Not surprisingly, many carnivore
 80 populations across the globe are threatened [27].

81 Carnivore species richness in Peninsular Malaysia is one of the highest in the world, with 31
 82 species representing seven families recorded to date [28] (Table 1). Sixteen (57%) of the
 83 remaining 28 species are listed as critically endangered, endangered, vulnerable, or near
 84 threatened at the global level [27]. The most recent local assessment of the conservation status
 85 of mammals lists 14 carnivore species as threatened or near threatened in Peninsular Malaysia
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87 **Table 1. Carnivores of Malaysia with 2015 IUCN conservation status, and Peninsular Malaysia conservation**
 88 **status in 2007 and 2009 based on percent change in area of occupancy and expert opinion [28].** Although 31
 89 species are listed, three species may not be indigenous or extant. The highest threat status, based on IUCN
 90 Red List criteria A–E [29] is reported for each species. EX = extinct, CE = critically endangered, EN =
 91 endangered, VU = vulnerable, NT = near threatened, LC = least concern.

	Family	Species	Common name	IUCN 2015 Red List status	Peninsular Malaysia 2009 Red List status ^a
1	Canidae	<i>Cuon alpinus</i>	Dhole	EN	NT
2	Felidae	<i>Panthera tigris</i>	Tiger	CE ^b EN	EN
3	Felidae	<i>Panthera pardus</i>	Leopard	NT	EN
4	Felidae	<i>Neofelis nebulosa</i>	Clouded leopard	VU	NT
5	Felidae	<i>Pardofelis marmorata</i>	Marbled cat	NT	LC
6	Felidae	<i>Prionailurus bengalensis</i>	Leopard cat	LC	LC
7	Felidae	<i>Prionailurus viverrinus</i>	Fishing cat ^{cb}	EN	VU
8	Felidae	<i>Prionailurus planiceps</i>	Flat-headed cat	EN	NT
9	Felidae	<i>Catopuma temminckii</i>	Asian golden cat	NT	LC
10	Herpestidae	<i>Herpestes javanicus</i>	Javan mongoose	LC	LC
11	Herpestidae	<i>Herpestes edwardsii</i> ^b	Indian gray mongoose ^{de}	LC	EX
12	Herpestidae	<i>Herpestes brachyurus</i>	Short-tailed mongoose	LC	LC

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13	Herpestidae	<i>Herpestes urva</i>	Crab-eating mongoose	LC	EN
14	Mustelidae	<i>Martes flavigula</i>	Yellow-throated marten	LC	NT
15	Mustelidae	<i>Mustela nudipes</i>	Malay weasel	LC	NT
16	Mustelidae	<i>Aonyx cinerea</i>	Asian small-clawed otter	VU	LC
17	Mustelidae	<i>Lutra sumatrana</i>	Hairy-nosed otter	EN	LC
18	Mustelidae	<i>Lutra lutra</i> ^c	Eurasian otter ^{ed}	NT	EN
19	Mustelidae	<i>Lutrogale perspicillata</i>	Smooth otter	VU	LC
20	Prionodontidae	<i>Prionodon linsang</i>	Banded linsang	LC	NT
21	Ursidae	<i>Helarctos malayanus</i>	Malayan sun bear	VU	VU
22	Viverridae	<i>Viverricula indica</i>	Small Indian civet	LC	NT
23	Viverridae	<i>Viverra zibetha</i>	Large Indian civet	NT	NT
24	Viverridae	<i>Viverra megaspila</i>	Large spotted civet	VU	EN
25	Viverridae	<i>Viverra zibetha</i>	Large Indian civet	NT	NT
26	Viverridae	<i>Cyanogale bennetti</i>	Otter civet	EN	EN
27	Viverridae	<i>Paguma larvata</i>	Masked palm civet	LC	LC
28	Viverridae	<i>Paradoxurus hermaphroditus</i>	Common palm civet	LC	LC
29	Viverridae	<i>Hemigalus derbyanus</i>	Banded civet	NT	LC
30	Viverridae	<i>Arctogalidia trivirgata</i>	Small-toothed palm civet	LC	LC
31	Viverridae	<i>Arctitis binturong</i>	Binturong	VU	LC

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147[28]

148 [IUCN changed status of tiger from endangered to critically endangered in 2015](#)

149^b Evidence for an indigenous population in Peninsular Malaysia is inconclusive [30,31].

150^c Considered introduced with records only from the west coast of the peninsular; no recent records [32].

151^d No proof that the species existed in Peninsular Malaysia [33], but Azlan and Sharma [34] reported a road kill in

152 Terengganu.

153 Carnivores are difficult to study by direct observation because many are nocturnal and
 154 secretive, and exist at intrinsically low population densities [35]. Early surveys in Peninsular
 155 Malaysia used traps, direct observation, signs, and road kills to infer species presence.
 156 Technological advances such as remote cameras have made it possible for recent surveys to
 157 document a greater variety of carnivore species and make inferences about their behavior,
 158 habitat use, distribution, and community composition [36–39]. All these techniques have their

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159 limitations, but collectively can provide useful information about where a species occurred, its
160 frequency or rarity of occurrence, and its possible vulnerability or adaptability to land use
161 change.

162 The demand for tropical forest products or land for agriculture continues to exert enormous
163 pressure on natural forests in Peninsular Malaysia. The conversion of tropical rainforest
164 includes small-scale swidden agriculture, rural and urban expansion, and large-scale
165 commercial agriculture [40,41]. A major cause of tropical forest loss has been the conversion of
166 secondary forest to industrial plantations including oil palm and rubber [42–45]. Future changes
167 in land use are inevitable as human populations grow and the country seeks further economic
168 development through commerce in agriculture and timber extraction. Although Southeast Asia
169 has few documented carnivore extinctions as a region [46], local extinctions of multiple forest-
170 dependent species have presumably occurred. Ranges of some species will likely shrink and
171 fragment, predisposing those remaining populations to even greater extinction risk [47]. For
172 example, tigers (*Panthera tigris*), a valuable species to gauge the success of landscape
173 conservation, are experiencing substantial range contraction in Peninsular Malaysia due to high
174 rates of human-induced changes to the landscape and increased poaching pressure [48,49].
175 However, we know little about the status and ecological requirements of the vast majority of
176 carnivores in Peninsular Malaysia, nor where the most sensitive and diverse carnivore
177 communities are likely to persist.

178 Here, we identify regions of high priority for carnivore conservation in Peninsular Malaysia, and
179 associated landscape factors. Using data on carnivore species distributions from published
180 surveys and records in combination with geographic information systems (GIS) data on
181 landscape variables, we 1) identify priority regions for carnivore conservation and 2) determine
182 associated environmental and anthropogenic landscape gradients.

183

184 **Methods**

185 **Study area**

186 Peninsular Malaysia (130,598 km²) is located within the Sundaland subregion of tropical East
187 Asia, which includes Borneo, Sumatra, ~~and~~ [Java, and surrounding islands, including Bali](#) [50]. In
188 December 2015, human population size was over 24 million with population densities
189 (excluding Federal territories) ranging from 40 individuals/km² in Pahang to 1600/km² in Penang
190 [51]. Malaysia's climate is typical of the tropical Sundaland subregion with abundant rainfall and
191 warm temperatures that fluctuate little throughout the year. The principal vegetation of tropical
192 rainforest dominated by Dipterocarps is floristically the richest of all the world's forests [46,52].
193 The nation's economy is based on minerals, particularly oil and tin, and agricultural produce;
194 rice and food crops are mainly for domestic consumption, but rubber, palm oil, and timber are
195 the principal earners of foreign exchange [52]. Conversion of tropical forest to other forms of
196 land use has been rapid in Malaysia. In a 30-year period, dryland forest declined from 64% of
197 Peninsular Malaysia's total area to less than 50% by 1990 and swamp forests declined from 14%

198 to 8% [52]. Over a 30-year period (1975–2005), 3.6 Mha of land were converted to oil palm
199 plantations, resulting in a 20% reduction in forest cover [53]. Rubber plantations that yield both
200 latex and timber are rapidly expanding to replace natural forests designated for timber
201 production under sustained yield, and 375,000 ha of monoculture timber are projected to
202 replace natural rainforest habitat by 2020 [44].
203

204 Literature search and data treatment

205 We first obtained a species list of carnivores in Peninsular Malaysia [28]. Next, we carried out a
206 literature search for carnivores in the country using scientific and common names, and including
207 more general search terms (mammal, vertebrate, or carnivore), for all available years up to and
208 including 2015 and one early 2016 publication ([see S11 Materials1Appendix](#)). We used
209 Thomson Reuter’s Web of Science to identify indexed papers, and the Malaysian Citation Centre
210 (<http://www.myjournal.my/public/browse.php>) to search journals in all biological categories. For
211 non-indexed Malaysian Journals without online search capability, we manually checked journal
212 contents and excluded papers/records that were not from Peninsular Malaysia. Our final data
213 set was derived from 85 published papers and reports (Fig 1, [S21 Materials2Appendix](#)) in the
214 English language with carnivore records based on live captures, direct observations, signs,
215 remote cameras, or road kills and other reported records from oldest to the most recent (1948
216 to 2014). Where publications did not provide coordinates of species records, we used an
217 estimate of the center of the study area for georeferencing. We recorded the date of the study,
218 location, and principal habitat types. Some studies were conducted in multiple geographic
219 locations; thus the number of geographic locations ($n = 89$) exceeded the number of papers or
220 reports, and some geographic locations were surveyed more than once. We mapped recent
221 (1991–2014) and older (prior to 1991) records by species, family, and IUCN Red List category.
222 We used 1991 as the cut-off year because most major land-use changes have occurred since
223 then. We used Kendall’s tau-b to explore associations among the number of records (all years)
224 per species, body size, global (IUCN) and Peninsular Malaysia threat status [27, 28], and habitat
225 breadth (number of different habitat types where a species was recorded). We weighted threat
226 status for each species based on an interval scale of 1 (LC; least concern), 2 (NT; near
227 threatened), 3 (VU; vulnerable), and 4 (EN ;[or CE](#); endangered [or critically endangered](#)
228 [respectively](#); see Table 1). We tested the hypothesis that threat status was negatively correlated
229 with habitat breadth. We assessed eight broad habitat types reported in the literature ([S2 Table](#)
230 [2](#)) and used species with ≥ 8 records to assess associations with habitat breadth. Because
231 riparian habitats were nested within most other habitats, they were not considered a separate
232 habitat type for this analysis.

233

234 **Fig 1. Procedure for the selection of studies of mammalian carnivores in Peninsular Malaysia with**
235 **records collected during 1948–2014.**

236

237 Identifying priority conservation areas

238 We used the georeferenced species data for the period 1948–2014 to identify clusters of
239 locations (i.e. hotspots) with carnivore assemblages for which conservation priorities were high
240 [54,55]. Many studies identified in our review were suitable for this objective because they
241 were broad-based mammal surveys. However, we excluded 25 papers where carnivore species
242 could not be linked with identifiable locations (a study area or geographic coordinate), or where
243 records were duplicates from other publications. Thus, we used data from 60 papers for the
244 hotspot analysis (Fig 1, S2 [MaterialsAppendix](#)).

245 [Our primary aim was to identify regions in the Malay peninsula that had high concentrations of](#)
246 [species that were globally threatened. Thus, f](#)For the hotspot analysis, we weighted
247 conservation priority for each species according to IUCN Red List status [27] based on an
248 interval scale of 1 (LC), 2 (NT), 3 (VU), and 4 (EN) as previously described. Using this scale value
249 as a weighting factor, we calculated the Getis-Ord G_i^* statistic in ArcGIS, which is a z-score that
250 provides a spatial statistic of where high or low values of the weighting factor occur [54]. This
251 approach allowed us to identify areas where species of greater (high z-scores; hotspots) or
252 lower (low z-scores; coldspots) global conservation concern were concentrated, which helped
253 reduce potential bias due to where surveys were conducted [56]. To calculate the z-scores, we
254 used inverse-squared Euclidean distances to measure spatial relationships among the values of
255 the weighting factor. This relationship allowed nearby carnivore observations to have greater
256 influence on computations for a target location than observations further away, with the
257 influence declining as a quadratic function of distance. The largest distance between two
258 nearest species records was 85 km so we used that distance as a search radius to ensure that
259 any unique survey location had at least one neighboring survey location. We used a kernel
260 density estimator in ArcGIS, again with a search radius of 85 km, to create a continuous surface
261 map of the z-scores.

262 Finally, we examined relationships between the z-scores and the landscape variables to gain
263 insights into which landscape gradients may be associated with areas where carnivore species
264 with high conservation rankings are concentrated as opposed to depleted. We examined
265 whether the z-scores were associated with the following environmental and anthropogenic
266 landscape gradients: elevation, natural land cover, human population density, proximity to
267 nearest town or village, and density of primary roads ([S1 Dataset](#)). We obtained elevation (m)
268 data from the Consortium for Spatial Information (<http://srtm.csi.cgiar.org/>). We reclassified
269 land-cover data from the Global Land Cover Database
270 (<http://forobs.jrc.ec.europa.eu/products/glc2000/legend.php>) into a binary layer to represent
271 all natural land cover types, excluding urban, cultivated, and managed areas. We then used a
272 neighborhood analysis to calculate the proportion of natural land cover within a radius of 15
273 km. We chose 15 km to reflect the large scale of our analysis and to ensure that values covered
274 the full range of very low up to 100% natural land cover. We obtained human population data
275 (counts per 30-arc grid cell, or approximate density/km²) from a Global Population Distribution
276 database (<http://www.ciesin.org/>). We calculated proximity to the geographic center of the
277 nearest town or village digitized from Google Maps. Finally, using the line density function in

278 ArcGIS, we calculated density of improved roads (km/km²; digitized from Google Maps) based
279 on a moving window with a 15-km radius. Land cover and human population data were from
280 2000, which was the approximate mid-point of the period during which most carnivore
281 observations were recorded. In addition to these environmental and anthropogenic variables,
282 we considered a variable that may have affected the sampling distribution, namely proximity to
283 the capital, Kuala Lumpur. Because of logistical considerations, many early surveys were
284 conducted in relatively close proximity (~100 km) to the capital (we used the GPS coordinates
285 of the headquarters of the Department of Wildlife and National Parks as our reference point).
286 This area has relatively high densities of improved roads, therefore we added an interaction
287 effect between road density and proximity to headquarters to every model to account for
288 potential sampling bias. Given the large spatial scale of our assessment, we set the resolution of
289 all data layers to 30-arc seconds for Peninsular Malaysia.

290 To explore potential relationships between the Getis-Ord G_i^* z-scores and landscape variables,
291 we used ordinary least squares linear regression in ArcGIS to examine a set of models with
292 different combinations of the environmental and anthropogenic variables to assess their
293 relative influence. We used proximity to Kuala Lumpur, improved road density and their
294 interaction as the basis for model building, to account for spatial sampling biases and reduce
295 spatial autocorrelation [57]. We used the bias-corrected Akaike's information criterion (AIC_c) for
296 model selection and considered models within $2 \Delta AIC_c$ values to be parsimonious [58]. To
297 reduce skewness in the data, we log-transformed human population and proximity to Kuala
298 Lumpur and square-root transformed improved road density. We tested for normal distribution
299 of residuals using the Jarque-Bera statistic. We used Koenker's studentized Bruesch-Pagan
300 statistic to determine if explanatory variables had a consistent relationship with Getis-Ord G_i^*
301 z-scores in geographic space and data space; if this test was significant, we calculated robust
302 standard errors, t -values, and probabilities for beta values. Finally, we tested whether model
303 residuals showed spatial autocorrelation based on Moran's I statistic.

304

305 Results

306 Records of distribution and habitat

307 Observation records spanned the period 1948–2014 with 96% collected during the last 50 years
308 and 50% collected after 1991 (Fig 2, S2 Table). We mapped all survey locations by family and
309 species (S1–S4 Figs) and by threat category (S5–S7 Figs). Recent survey records (i.e., since 1991)
310 in largely primary rainforest in northern Perak revealed high carnivore species richness. In
311 Selangor, 75% of carnivore records preceded 1991, thus fewer surveys may have influenced the
312 relative paucity of recent versus older carnivore records (S1–S6 Figs). Records were few (<5) for
313 10 species, almost all of which were small to medium-sized carnivores (Fig 3) and there were no
314 recent records of the endangered otter civet (*Cyanogale bennettii*). The number of records
315 tended to be greater with species' body size (Kendall's tau-b = 0.24, $z = 1.78$, $P = 0.038$), but not
316 with IUCN global or Peninsular Malaysia conservation scores.

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317 **Fig 2. Distribution of surveys ($n = 133$) of carnivores among different states in Peninsular Malaysia**
318 **with records collected during 1948–2014.** Data were based on 60 published papers and reports that
319 used conventional trapping, direct observation, signs, remote cameras, or road kills. Some publications
320 compiled data from several surveys and some geographic locations were surveyed more than once.
321 [Boundary layers: Esri, Garmin International \(formerly DeLorme Publishing Company, Inc.\), Inc.;](#) [Inset](#)
322 [map: U.S. Central Intelligence Agency \(The World Factbook\).](#)

323
324 **Fig 3. Number of records of Carnivora species in Peninsular Malaysia.** Data were obtained from surveys
325 that used conventional trapping, direct observation, sign, remote cameras, or road kills collected during
326 1991–2014. Species are grouped by family and ranked by number of records.

327 Surveys (or specimens collected) in forest reserves, wildlife reserves and national parks
328 consisting mostly of dry-land forest comprised 75% of the reports. The remaining reports were
329 from rice fields (12%), peat swamp/mangrove forest (6%), oil palm plantations (3%), mangrove
330 forests (2%) and human inhabited areas (2%). We used carnivore species presence data from 89
331 geographic locations to examine habitat types associated with species records (S2 Table).
332 Habitat breadth was associated with the number of records per species (Kendall's tau-b = 0.554,
333 $z = 3.03$, $P = 0.001$), but not with species' IUCN global or Peninsular Malaysia conservation
334 scores, or with body size.

335 Priority conservation areas

336 A region in the northeastern portion of the peninsula had the greatest concentration of
337 carnivores with high conservation status, within which two areas were particularly prominent:
338 the forest complex associated with Royal Belum State Park in the northern portion of this region
339 and, southeast of it, an area associated with Taman Negara National Park (Fig 4). Notably, we
340 also identified a concentrated area with carnivore observations and diversity associated with
341 the southern half of Selangor and the adjacent region in Pahang, including Krau Wildlife
342 Reserve, but the presence of carnivores with high conservation status was much lower
343 compared with other areas.

344
345 **Fig 4. Locations of mammalian carnivore surveys and kernel density surface of Getis-Ord G_i^* z-scores**
346 **of weighted ranking of IUCN red list categories for recorded species locations in Peninsular Malaysia,**
347 **1948–2014.** [Hillshade layer derived from Shuttle Radar Topography Mission \(STRM\) 90-m Digital](#)
348 [Elevation Data from Consultative Group on International Agricultural Research \(CGIAR\) and reprinted](#)
349 [under a CC BY license, with permission from International Center for Tropical Agriculture \(CIAT\), original](#)
350 [copyright 2004.](#) Protected areas mentioned in the text are labeled; [reprinted from World Database on](#)
351 [Protected Areas \(<http://www.protectedplanet.net>\) under a CC BY license, with permission from the](#)
352 [United Nations Environmental Programme-World Conservation Monitoring Centre, original copyright](#)
353 [2010.](#)

354 Model selection of ordinary least squares regressions showed the best-fitting model included
355 elevation, proportion of natural land cover, improved road density, proximity to Kuala Lumpur,
356 and the interaction between the latter 2 variables (adjusted $R^2 = 0.62$; S1 Table). The second-

357 best model was within 2 ΔAIC_c values and contained human population density as an additional
358 variable. However, the 95% confidence interval of that variable overlapped zero so we focused
359 our interpretation on the top model. The Jarque-Bera (*JB*) statistic indicated the residuals of the
360 model did not deviate from normality (*JB* = 0.459, 2 df, *P* = 0.797). Getis-Ord G_i^* z-scores were
361 negatively associated with elevation (β = -0.00124, SE = 0.00057, *t* = -2.169, *P* = 0.042) and
362 positively associated with proportion of natural land cover (β = 1.899, SE = 0.711, *t* = 2.671, *P* =
363 0.009) and distance to Kuala Lumpur (β = 1.811, SE = 0.339, *t* = 5.344, *P* < 0.001). Thus, areas
364 where observations of species with higher conservation ranks were spatially clustered generally
365 coincided with areas at lower elevations, with greater proportion of natural land cover, and
366 tended to be more distant from Kuala Lumpur. Human population density and proximity of the
367 nearest town or village did not show an association with the Getis-Ord G_i^* z-scores. There was
368 some evidence of spatial autocorrelation among the residuals (Moran's *I* = 0.461, *z* = 2.018, *P* =
369 0.044).

370

371 Discussion

372 Peninsular Malaysia contains possibly the greatest number of native species of Carnivora within
373 Sundaland, and more than half are globally threatened or near threatened. Using data compiled
374 from the first comprehensive review of publications with carnivore records, we identified two
375 regions that overlapped with protected areas, Taman Negara National Park and Royal Belum
376 State Park, as hotspots for carnivore species of greatest conservation concern.

377 Both these protected areas are considered priority areas for tiger conservation in Malaysia [59].
378 Established in 1938, Taman Negara (4343 km²) is Malaysia's oldest national park [60] and
379 comprises portions of ~~three the S~~states of Pahang, Terengganu, and Kelantan. It contains
380 Malaysia's largest continuous tract of primary forest, of which nearly 60% consists of low
381 elevation (75–300 m) rainforest. Royal Belum State Park, however, was gazetted ~~in relatively~~
382 ~~recently-2007~~ [61] and is part of the Belum-Temengor Forest Complex (3546 km²) located in
383 northern Perak; it shares its northern boundary with Thailand, where it connects with two
384 protected areas, Hala Bala Wildlife Sanctuary and Bang Lang National Park. The combined
385 extent of protected areas and forest reserves in this forest complex, which consists of lowland
386 and hill dipterocarp forests from 130 to 1500 m ~~[61]~~, is said to rival that of Taman Negara [62].
387 The number of carnivore species reported in Taman Negara and Belum-Temengor were 19 and
388 22, respectively, each with eight threatened and five near-threatened species.

389 A crucial finding was the relative scarcity of reports of carnivores of conservation concern in the
390 southwestern region of the Peninsular encompassing the state of Selangor and the adjacent
391 region in the state of Pahang, despite frequent surveys in that area. The surveys were
392 conducted within a 50- to 60-km radius of Kuala Lumpur, where several small forest reserves
393 and areas (12–200 ha) of secondary forest have existed within the city limits for decades, with
394 more extensive lowland and hill dipterocarp forests in peri-urban areas [63]. Surveys in this

395 region occurred over a long time span, with over half the records collected prior to 1991. The
396 distinct paucity of records of carnivores of conservation concern suggests that many of these
397 species cannot persist in small fragmented habitats, or even in larger extents of habitats close to
398 urbanization. Krau Wildlife Reserve (603 km²), situated within a 1556-km² forested area [64],
399 was the largest protected area in this coldspot. Krau Wildlife Reserve is surrounded by
400 agriculture and settlements, but its northeastern boundary is < 50 km south of the large
401 forested landscape of Taman Negara. It was thus considered a secondary priority site for tiger
402 conservation in Malaysia [65]. Carnivore species richness in Krau ($n = 20$) was similar to that
403 reported at Belum-Temengor and Taman Negara, although with fewer threatened ($n = 5$) and
404 near threatened species ($n = 4$).

405 Carnivore hotspots were associated with large extents of natural land cover, lower elevations,
406 and greater distances from Kuala Lumpur, within the state of Selangor. Selangor (800,000 ha),
407 the most populous state in Malaysia with 5.8 million people [66] has the highest per capita GDP,
408 and has experienced the most rapid growth in the manufacturing sector in the last five decades.
409 Urban and agricultural development has been responsible for most of the state's change in land
410 use with the expansion of oil palm plantations at the expense of peat swamp forest [42, 67].
411 Considering that 75% of the surveys in Selangor were conducted before 1991, [and our human](#)
412 [population and land use data were derived more recently](#), the status of carnivore populations in
413 this state may be more critical than the data suggest.

414 A common consequence of urbanization and development is habitat fragmentation and the
415 extirpation of large apex predators. Laidlaw's [68] survey of seven sites (70 to >10,000 ha) in
416 Peninsular Malaysia suggested that large tracts of natural forest were the most important
417 predictor of mammal species richness and large carnivore presence. Woodroffe [16]
418 demonstrated a strong positive relationship between reserve size and the persistence of large
419 carnivores and concluded that smaller habitat patches increased the potential for human-
420 carnivore conflicts with subsequent extirpation of local carnivore populations. Many small and
421 mid-sized carnivores also rely on larger habitat patches suggesting that factors other than body
422 size, such as resource specialization, behavior, and social structure, may play an important role
423 in this dependency [16, 69]. Smaller habitat patches could mean the loss of suitable habitat,
424 new barriers to movement, or competition with species better adapted to disturbed
425 environments [70]. Proximity to urbanization and primary roads, even where habitat is
426 sufficiently large, limits dispersal and enhances the risk of road mortality and illegal hunting
427 [71–73].

428 Low-elevation habitats with natural forest cover may be one of the most valuable habitats for
429 carnivores in tropical regions. We found that all but two species of Carnivora were reported in
430 lowland forests (S2 Table). Notably, the number of species of Carnivora reported in lowland
431 swamp forests ($n = 17$) was high, considering the relatively few surveys ($n = 16$). In Southeast
432 Asia, lowland equatorial forests support the vast majority of species [46] and in Peninsular
433 Malaysia, lowland forests support almost 90% of mammal species with 61% occurring only in

434 lowland and hill forests below 1000 m [74]. Malaysia has lost nearly 40% of its original forest
435 cover [75] and recent annual deforestation rates in the peninsula (0.9% annually from 2000 to
436 2010 [46]) show little sign of abatement.

437 With the exception of the otter civet (one record in 1987), records since 1991 exist for the
438 remaining 27 species in the peninsula. Records were few for nine species, mostly small
439 carnivores, including four species of Viverridae and all three species of Herpestidae native to
440 the Malay Peninsula. We found only one record of the Javan mongoose (*Herpestes javanicus*)
441 and one of the small Indian civet (*Viverricula indica*) since 1991; these species are neither
442 globally threatened nor near threatened. Conversely, records were greater for larger species
443 such as the tiger, sun bear (*Helarctos malayanus*), and leopard (*Panthera pardus*). In an
444 extensive review of carnivore research effort, [76] reported a strong association between body
445 size and research effort in the Carnivora, with the Viverridae and Herpestidae among the four
446 least studied of the carnivore families. Larger species leave more definitive signs and range over
447 larger areas, thus increasing the probability of detection. Also, the rarely recorded Javan
448 mongoose and small Indian civet favor open, less forested habitats (77,78); apart from rice
449 fields, these habitats are rare in Peninsular Malaysia. The dearth of ecological studies on
450 smaller carnivores in peninsular Malaysia may predispose them to early extinction, when
451 efforts for their conservation are less costly than for large-bodied species, and more likely to
452 succeed [79].

453 Large body size confers greater vagility and thus the ability to use a wide array of habitats but
454 we found no association between habitat breadth and body size. Also, species that use a wide
455 range of habitats may be more tolerant of habitat loss and fragmentation [80]. Although there
456 may be some sampling bias given that species with more records were reported in more
457 habitats, habitat breadth was not associated with global (IUCN) or local (Peninsular Malaysia)
458 threat status. To illustrate, three small carnivores, the common palm civet (*Paradoxurus*
459 *hermaphroditus*; least concern), the leopard cat (*Prionailurus bengalensis*; least concern), and
460 the flat-headed cat (*Prionailurus planiceps*; endangered) were reported in a wide variety of
461 habitats (S2 Table), including small forest patches in urban landscapes. The flat-headed cat is
462 adapted for feeding on aquatic prey, thus the presence of wetland habitat, which is abundant in
463 Peninsular Malaysia, may be more important for its persistence than forest cover. Locally, the
464 flat-headed cat is considered near threatened [28], in contrast with its global endangered status
465 [27], which may reflect its ability to persist in a variety of habitats associated with freshwater.

466 We acknowledge several caveats in our study. Despite our attempt to obtain as complete a set
467 of published studies for our analysis as possible, at least three papers with nine additional
468 records of leopard [81,82] and one record of a flat-headed cat [83] escaped our attention. ~~Of~~
469 ~~However, if we included these 10 records, including~~ 29 recently released records of threatened
470 and near threatened carnivores [84–87], ~~82% 82% of records~~ occurred within the hotspots
471 identified in our analysis, confirming the importance of these regions for carnivore
472 conservation. We caution, however, that despite demonstrating distinct landscape associations

473 with the distribution of carnivores as weighted by their conservation rankings, we could not
474 fully account for spatial autocorrelation and our data were not derived from standardized,
475 probabilistic, or systematic coverage of the entire peninsula. Thus, our inference is weaker in
476 areas with fewer surveys and published records. For example, the data included few surveys for
477 the southern region of the peninsula, including the Endau Rompin Forest Complex (~2389 km²).
478 ~~This area with comprises~~ substantial low-elevation rainforest ~~that likely supports with the~~
479 ~~potential to support~~ a diversity of indigenous carnivores ~~despite its~~. ~~Endau Rompin was~~
480 ~~considered low priority for tiger conservation owing to~~ highly fragmented surroundings areas
481 and poor connectivity with large, forested landscapes [65]. ~~Nevertheless,~~ A recent remote
482 camera survey reported the presence of six felid species, including tigers [88].
483

484 Conclusion

485 Peninsular Malaysia supports several species of globally threatened carnivores and our study
486 underscores the importance of natural forest cover for their persistence. We show that
487 carnivores of greatest conservation concern are less likely to persist in small, fragmented
488 habitats or habitats close to urban areas. Recent (2000–2012) changes in global forest cover
489 indicate that Malaysia lost 14% of its forest cover, a rate of loss that exceeded any other
490 country [89]. Oil palm and industrial timber plantations replaced most of the lost forest [90]
491 and trends point to their continued expansion. Surveys and targeted ecological studies of
492 carnivores in habitat types other than primary and secondary forests will thus be important to
493 elucidate their status and capacity to persist in the face of progressive habitat alteration.
494 Recent studies in oil palm estates and commercial forest plantations suggest that these altered
495 habitats may serve as ecological corridors and shelter valuable elements of biodiversity [91–93],
496 but primarily when interspersed with large (>1000 ha) stands of natural, secondary forest [94].
497 Ultimately, reducing poaching and habitat loss within large, contiguous stands of rainforest will
498 be crucial for the persistence of Malaysia’s most threatened carnivores and consequently the
499 broader ecological communities that carnivores influence.

500

501 Supporting information

502 [S1–7 Figures. Recent \(1991–2014\) and older \(1948–1990\) records of carnivores by family and](#)
503 [IUCN threat status in Peninsular Malaysia.](#)

504 [\(.docx\)](#)

505 [S1 Table. Model selection results to identify landscape variables associated with spatial](#)
506 [clustering of carnivore records based on weighted ranking of IUCN red list categories.](#)

507 [\(PDF\)](#)

508 [S2 Table. Carnivora species reported in Peninsular Malaysia and associated habitats, 1948–](#)
509 [2014.](#)

510 [\(PDF\)](#)

511 [S1 Appendix. Search terms and sources for carnivore records and habitats in Peninsular](#)
512 [Malaysia.](#)
513 [\(PDF\)](#)
514 [S2 Appendix. Records of Carnivora by species, locations, and year.](#)
515 [\(.xlsx\)](#)
516 [S1 Dataset. Geo-referenced TIFF files for spatial data layers used in landscape analysis.](#)
517

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525 [use of trade, firm, or product names is for descriptive purposes only and does not imply](#)
526 [endorsement by the U.S. Government.](#)
527

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