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ORIGINAL RESEARCH

# Identifying gaps in the conservation of small wild cats of Southeast Asia

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**Abstract**
Southeast Asia hosts more felid species than any other region and, although smaller (< 30 kg) felids have important ecological roles, regional conservation has mainly focused on a few charismatic big cats. Information on the ecology and conservation status of small felids is often lacking or geographically limited. We used empirically derived scale-optimized models for seven species in three regions of Southeast Asia (mainland, Borneo and Sumatra) to evaluate the effectiveness of the existing protected areas network in preserving suitable habitats, and to map suitable areas lacking protection. Finally, we assessed whether small felids are good proxies of broader regional terrestrial biodiversity. On the mainland, the largest and most suitable habitats occurred in the Northern Forest Complex of Myanmar and in the region between Eastern Myanmar, Laos and Vietnam. In these areas we also highlighted the most important protected areas. In Borneo, the most suitable habitats occurred in the central highlands and in the protected areas of Sabah. In Sumatra, the strongholds of habitat suitability were the Barisan Mountains, in the western extent of the island, and were highly concentrated within existing protected areas. We also found that the aggregated habitat suitability for small felids was correlated more strongly to terrestrial vertebrate biodiversity than was any single felid species individually, suggesting that areas that are suitable for multiple felid species have an association with high overall biodiversity. Overall, our assessment of the distribution of small felids in Southeast Asia highlights the fundamental importance of protected areas for biodiversity conservation, given that most species were highly associated with protected areas and regions with large extents of forest. Our results are a clarion call to expand the extent, and improve the conservation management, of protected areas in the remaining core habitat areas for multiple species in Southeast Asia, and to work to enhance and protect connectivity between them to ensure long-term demographic and genetic exchange among the region's remaining wildlife populations.

**Keywords** Gap analysis · Protected area effectiveness · Felids · Generalised linear model · Multi-scale model optimisation · Multi-species model · Random forest · Species distribution modelling

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Communicated by Xiaoli Shen.

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Luca Chiaverini and David W. Macdonald are joint first authors.

## Introduction

Southeast Asia has the highest deforestation rates globally (Hughes 2017) and the conditions driving high deforestation rates are likely to persist and increase over the next decade or more (Meittinen et al. 2011; Cushman et al. 2017; Chen et al. 2024). If current rates of deforestation persist, Southeast Asia would lose three-quarter of its original forest cover by 2100 (Achard et al. 2002), with dramatic consequences for biodiversity, including a projected loss of between 24 and 63% of its terrestrial endemic species (Sodhi and Brook 2006).

Although habitat loss affects all taxonomic groups, carnivores are particularly vulnerable given their low fecundity, high habitat area requirements and high vulnerability to human persecution (Cardillo et al. 2004). As habitat loss and fragmentation reduce the availability of large, intact patches of suitable habitat, carnivores are frequently restricted to small, less suitable areas, often outside protected areas and embedded within human-dominated landscapes (Crooks et al. 2017; Cushman et al. 2018; Loveridge et al. 2022).

While large charismatic species in this region have received high attention from conservationists [e.g., orangutans (Pandong et al. 2019), tigers (Ash et al. 2021), leopards (Rostro-Garcia et al. 2016) and clouded leopards (Macdonald et al. 2018, 2019)], smaller species are largely under-studied [but see Macdonald et al. (2020) and Chiaverini et al. (2022)]. The relative paucity of information on the status of small carnivores in Southeast Asia, coupled with the regions rapid deforestation, amplifies the urgency of assessing their conservation status (Chiaverini et al. 2022; Macdonald et al. 2020).

Southeast Asia supports the largest number of sympatric felids of any region in the world (Macdonald and Loveridge 2010). Of these, tigers and leopards have been the main focus of past conservation efforts and economic investments (Brodie 2009; Macdonald et al. 2015), and clouded leopards have recently gained attention (Macdonald et al. 2018, 2019). Information for smaller felids is often lacking or limited to circumscribed geographic contexts (Haidir et al. 2018; Hearn et al. 2018; Rasphone et al. 2021; Rostro-Garcia et al. 2021). However, small felids have crucial ecological roles in the trophic structure of ecosystems (Roemer et al. 2009), and some of them can also take on the role of apex predators through ecological release when larger carnivores are extirpated (de Oliveira et al. 2010). Additionally, small felids have been revealed to be important indicator and sentinel species (Chiaverini et al. 2022; Cruz et al. 2019), likely due to their relatively fast rates of population change and to their direct responses to both bottom-up and top-down ecological processes (Marneweck et al. 2022).

In this paper we sought to develop the first regional assessment of habitat suitability and conservation status for Southeast Asia's small felids. By modelling habitat suitability individually for seven species of smaller felids (mainland *Neofelis nebulosa* and Sunda clouded leopards *Neofelis diardi*, Asiatic golden cat *Catopuma temminckii*, marbled cat *Pardofelis marmorata*, leopard cat *Prionailurus bengalensis,* Sunda leopard cat *Prionailurus javanensis*, and Borneo bay cat *Catopuma badia*, sampled in three regions (mainland, Borneo and Sumatra) we sought to: (1) predict the geographic distribution of smaller felids in Southeast Asia, (2) evaluate the effectiveness of the current systems of protected areas to preserve suitable habitats for smaller felids, (3) highlight the most suitable areas currently lacking protection and (4) assess whether small felids' suitable habitat was highly associated with geographic distribution of broader biodiversity richness in the region.

## Materials and methods

### Study area

The study area encompassed mainland Southeast Asia and the Sunda Islands of Borneo and Sumatra, extending between 5° S and 35° N latitude and 80° E–120° E longitude, and spanning a broad altitudinal gradient ranging from coastal areas to Himalayan peaks above 8000 m asl (Fig. 1). Thirteen countries were included in the study area, of which Bangladesh, Bhutan, Cambodia, Laos, Malaysia, Myanmar, Nepal, Singapore, Thailand and Vietnam were entirely encompassed within the area, and China, India and Indonesia were partially included (Fig. 1).

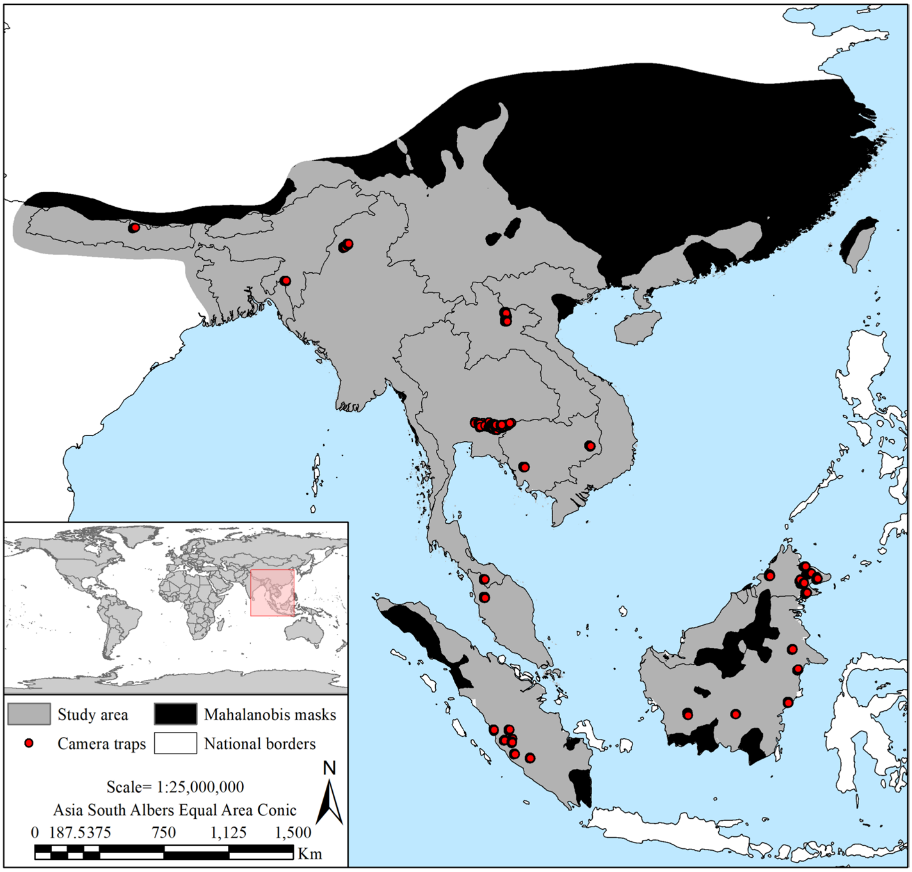


**Fig. 1** Map of the study area. Shown are the locations of the camera traps and the Mahalanobis masks produced to cover the regions too different from the sampling locations

## Mapping habitat suitability

Building on the methodology applied and discussed in Chiaverini et al. (2023), we produced habitat suitability models for the sampled felids by applying two different algorithms and, for each of them, two data re-sampling techniques, resulting in four different modelling frameworks. Specifically, we produced habitat suitability models by applying generalised linear model (GLM) and random forest (RF) and, for each of them, we trained the models by bootstrapping or not the training data. For each sampled smaller felid species, in each subregion (Mainland, Borneo, Sumatra), we selected the best model, defined by the highest AUC in the independent validation, from Chiaverini et al. (2023). Detailed information on the modelling approach and selected models are presented in the supplementary material to this manuscript. Additionally, we highlighted the most suitable areas for all of the study species jointly by combining by addition the single-species habitat suitability layers.

## Effectiveness of protected areas

We evaluated the effectiveness of the current protected area systems in mainland Southeast Asia, Borneo and Sumatra in preserving the hotspots of suitability for each individual felid species and all felids jointly. Using a pixel resolution of 250 m, we classified the habitat surface according to low suitability (50th to 70th percentile),, medium suitability (70th to 90th percentile) and high suitability (above the 90th percentile) (Chiaverini et al. 2022; Macdonald et al. 2018). Then, we constructed a measure the effectiveness of the protected areas by calculating the ratio between the extent of each suitability class (i.e., low, medium and high suitability, as specified above) encompassed within each protected area, and the extent of that class in the entire study area, independently for mainland Southeast Asia, Borneo and Sumatra. We believe this is a measure of protected area effectiveness, in the sense that it measures the effectiveness of protected areas in conserving the portions of the landscape that are most highly suitable for small felids. We obtained the protected area layer from the World Database on Protected Areas (UNEP-WCMC and IUCN 2022), and we consistently followed its structure without deleting, merging or altering the protected areas, thereby ensuring that our assessment is reproducible throughout the study area.

## Gap analysis

Focusing only on the medium and high suitability classes to emphasise the areas with the highest conservation value, we produced a gap analysis by highlighting the areas predicted to be important to felid diversity that fall outside the current systems of protected areas. We performed gap analyses independently for mainland Southeast Asia, Borneo and Sumatra.

## Felids as biodiversity indicators

To evaluate the effectiveness of small felids as biodiversity indicators, independently for each study area, we calculated Pearson's correlation coefficients between the most supported model for each felid and the species richness surfaces produced for mainland Southeast Asia and Sunda Islands, respectively, by Macdonald et al. (2020) and Chiaverini et al.

(2022). The rationale for this correlation analysis is that if a felid species is a strong overall biodiversity indicator its habitat suitability map should have a high spatial correlation with spatal patterns of multispecies biodiversity (such as reported by Macdonald et al. 2020, and Chiaverini et al. 2022). Additionally, for each study area, we also calculated the Pearson's correlation coefficients between the sum of habitat suitability layers across felids collectively and the species richness surfaces.

## Results

### Felid habitat suitability

Here we present an assessment of the protected areas effectiveness and gap analysis based on this summed suitability across smaller felid species (Figs. 2, 3, 4). In addition, we provide the single-species habitat suitability layers in Figs. S1–S12. For each of the three subregions (mainland, Sumatra, Borneo) the summed felid richness layer was highly related to the extent of remaining natural forest. Overall, most felid species have larger extents of remaining quality habitat in Borneo than in either Sumatra or mainland Southeast Asia. Much of the predicted quality habitat in Borneo is outside of and surrounding protected areas, while in Sumatra remaining quality habitat is highly fragmented and limited nearly exclusively to protected areas. A similar pattern is seen in the mainland, except for Northern Myanmar and adjacent areas of Laos where extensive predicted quality habitat still exists outside of protected areas.

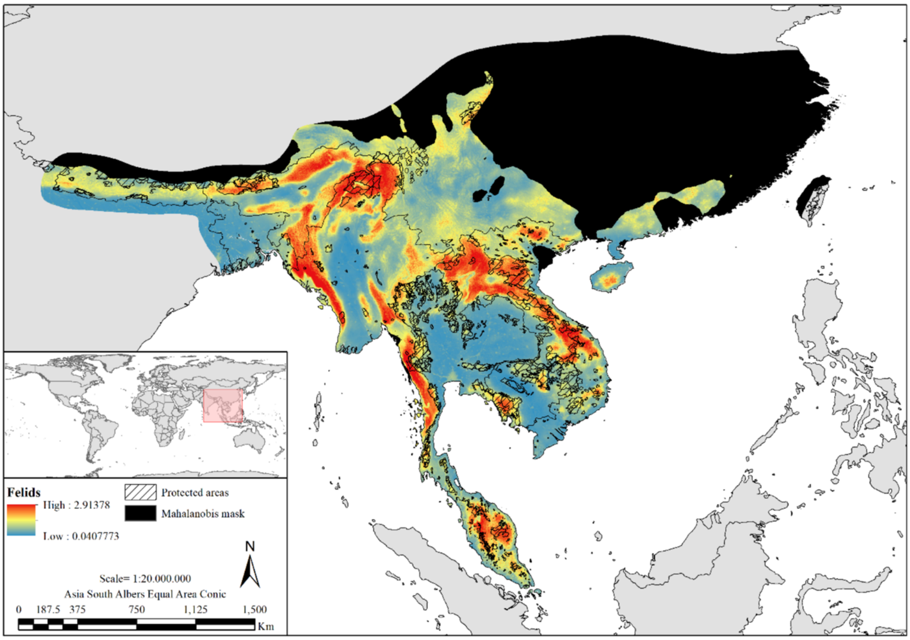


**Fig. 2** Species distribution probability surface of the sampled felid species in mainland Southeast Asia

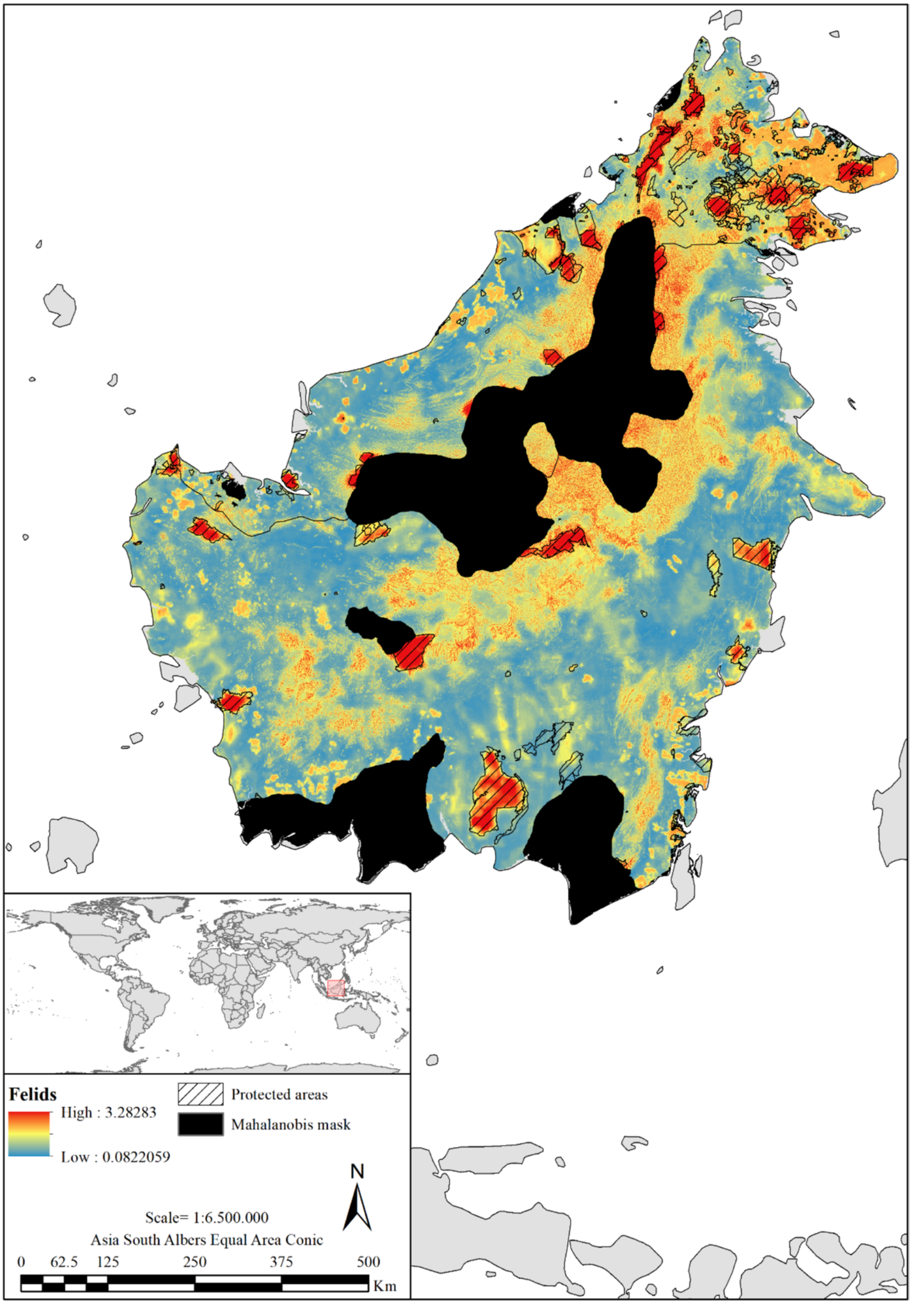


**Fig. 3** Species distribution probability surface of the sampled felid species in Borneo

In the mainland (Fig. 2) there were four main areas of high predicted richness of small felids, including: (1) a large area running up the west coast of Myanmar through the Northern Forest Complex, then westward along the front of the Himalayas through Asam,

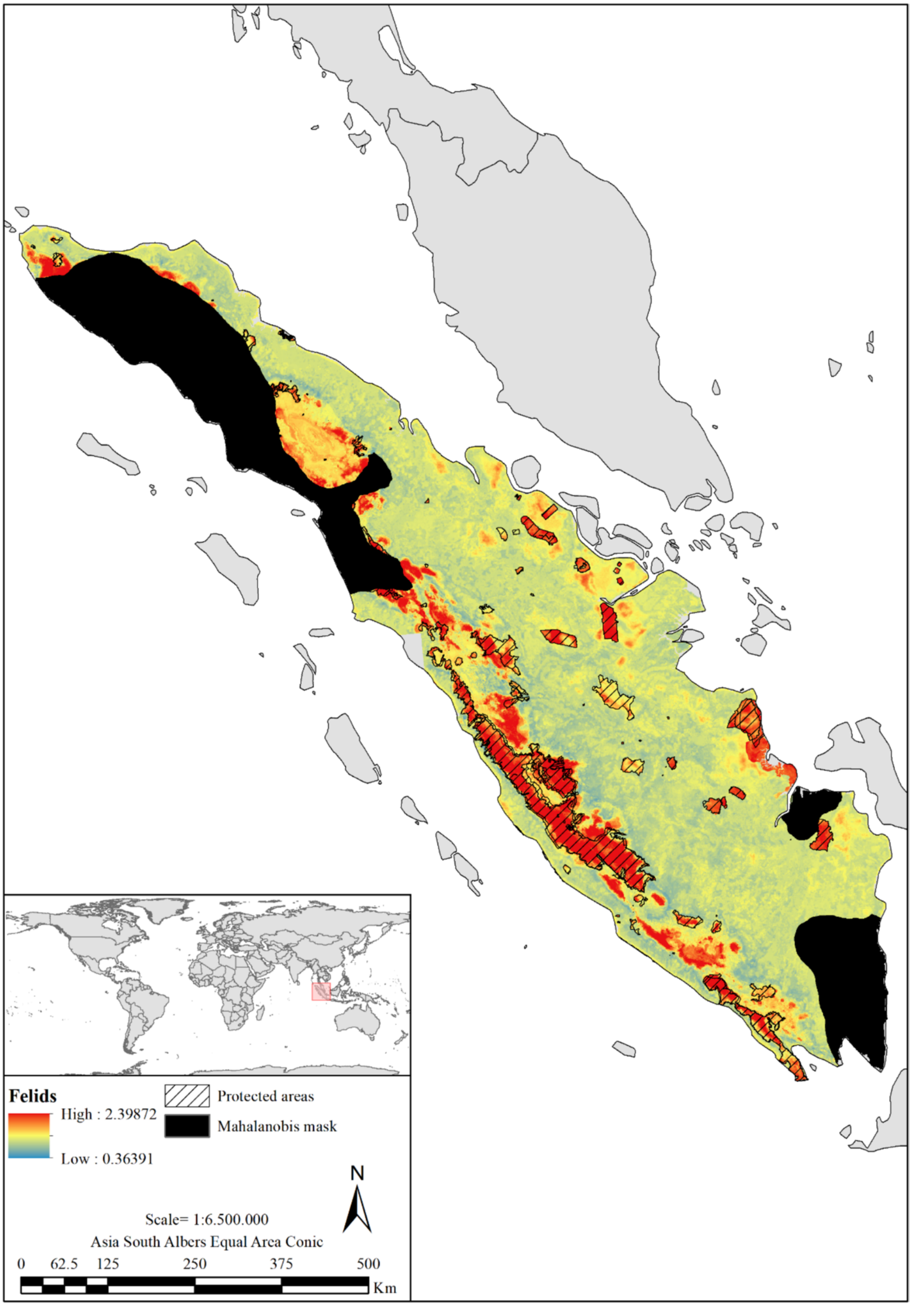


**Fig. 4** Species distribution probability surface of the sampled felid species in Sumatra

Bhutan and Nepal, (2) the Western Forest Complex along the border of Thailand and Southern Myanmar, (3) an extensive area running from the border of Myanmar and Laos eastward through most of Laos, and (4) much of the central part of Peninsular Malaysia surrounding Taman Negara. In Borneo areas of high multispecies occurrence probability of smaller felids were concentrated in the mountainous areas of Sabah and Kalimantan where extensive native forest remains, as well as lowland forest remnants associated with protected areas (Fig. 3). Similarly, in Sumatra areas of high predicted small felid richness were mainly concentrated in the forested regions of the mountain range running the length of the western coast of the island and small, lowland protected areas elsewhere on the island where forest remains (Fig. 4).

## Effectiveness of protected areas

In mainland Southeast Asia, several of the protected areas that were most effective in preserving highly suitable habitat for smaller felid conservation were located in the Northern Forest Complex of Myanmar (Fig. 5). Specifically, the protected area containing highly suitable habitat for the largest number of smaller felid species was Hukaung Valley Wildlife Sanctuary (extension), while Hukaung Valley Wildlife Sanctuary and Bumpha Bum Wildlife Sanctuary ranked as the third and fourth most effective protected areas, respectively (Table 1). The protected area identified as having second highest effectiveness (based on predicted multi-species habitat quality) most was the Western Nghe An UNESCO-MAB Biosphere Reserve, in Vietnam. Taman Negara (Pahang) National Park, in Malaysia had the fifth highest effectiveness rank, followed by Virajay National Park, (sixth rank), Central Kravanh (seventh rank), both in Cambodia. Rounding out the top 10 most effective mainland protected areas for small felid conservation effectiveness were the Taninthayi Nature

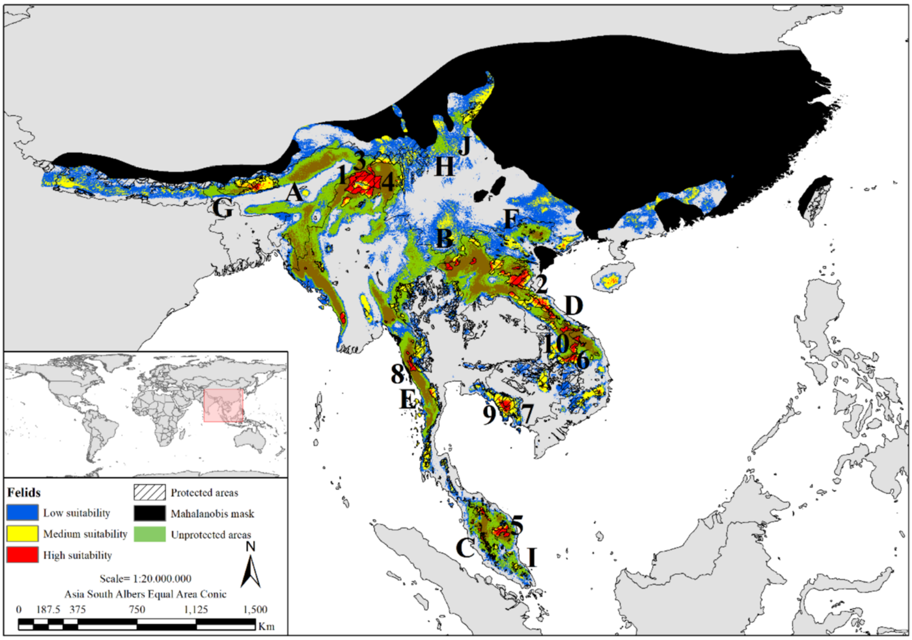


**Fig. 5** Reclassified probability surface of the sampled felid species in mainland Southeast Asia, showing areas with low, medium and high habitat suitability. Codes of the protected areas and of the unprotected suitable areas are reported in Tables 1 and 4, respectively

**Table 1** Main protected areas in terms of extent of high suitability habitat for the sampled felid species in mainland Southeast Asia

| Protected areas | Code | Country | Low suitability habitat (km$^2$) | Low suitability habitat (%) | Medium suitability habitat (km$^2$) | Medium suitability habitat (%) | High suitability habitat (km$^2$) | High suitability habitat (%) |
|---|---|---|---|---|---|---|---|---|
| Hukaung Valley Wildlife Sanctuary (extension) | 1 | Myanmar | 3.94 | 0.00 | 1305.31 | 0.19 | 9992.06 | 3.00 |
| Western Nghe An | 2 | Vietnam | 679.75 | 0.09 | 3278.00 | 0.47 | 5648.63 | 1.69 |
| Hukaung Valley Wildlife Sanctuary | 3 | Myanmar | 6.13 | 0.00 | 929.88 | 0.13 | 5553.88 | 1.67 |
| Bumpha Bum Wildlife Sanctuary | 4 | Myanmar | 0.00 | 0.00 | 5.69 | 0.00 | 2923.00 | 0.88 |
| Taman Negara (Pahang) | 5 | Malaysia | 0.00 | 0.00 | 614.94 | 0.09 | 2012.06 | 0.60 |
| Virajay | 6 | Cambodia | 138.13 | 0.02 | 1391.06 | 0.20 | 1774.13 | 0.53 |
| Central Kravanh | 7 | Cambodia | 58.81 | 0.01 | 2271.94 | 0.33 | 1675.81 | 0.50 |
| Taninthayi Nature Reserve | 8 | Myanmar | 0.00 | 0.00 | 5.25 | 0.00 | 1605.25 | 0.48 |
| Southern Kravanh | 9 | Cambodia | 486.88 | 0.07 | 1967.44 | 0.28 | 1583.75 | 0.47 |
| Dong Ampham | 10 | Laos | 0.00 | 0.00 | 413.06 | 0.06 | 1570.69 | 0.47 |

Reported are the extent of the low, medium and high suitability habitats occurring in each protected area, and the proportion of the extent of the suitability class over the extent of that class in mainland Southeast Asia

Reserve in Myanmar (eighth rank), South Kravanh National Park in Cambodia (ninth rank) and Dong Ampham National Protected Area in Laos (tenth rank).

In Borneo, we found that one-fourth of the highly suitable felid habitat was encompassed within the ten most highly effective protected areas (Table 2). The two effective protected areas for preserving multiple small felid habitat quality in Borneo were Sebangau National Park and Bukit Baka—Bukit Raya National Park, in the Indonesian provinces of Central and West Kalimantan (Fig. 6). Next in importance was Bukit Sapat Hawung Nature Reserve in the highlands of the central Borneo and Crocker Range National Park in Sabah (third and fourth rank, respectively). Tabin Wildlife Reserve and Kinabalu Park, also in Sabah, were sixth and eighth among the most effective Bornean protected areas. Among the areas protecting the largest extents of highly suitable habitat, we also identified Kutai National Park in East Kalimantan (fifth rank), Kayan Mentarang National Park in North Kalimantan (seventh rank), and Gunung Nyiut Penrissen Nature Reserve (ninth rank) and Gunung Palung National Park in West Kalimantan (tenth rank).

In Sumatra, our analysis highlighted the immense importance of Kerinci Seblat National Park and Bukit Barisan Selatan National Park (Fig. 7; Table 3). Next in importance were Kerumutan Wildlife Reserve (third rank), Padang Sugihan Wildlife Reserve (fourth rank) and Berbak National Park (fifth rank), all in the eastern coastal region of Sumatra, where we identified also Giam Siak Kecil Wildlife Reserve (seventh rank) as an important protected area for felid diversity. Bukit Rimbang Bukit Baling Wildlife Reserve and Arau Hilir dan Air Terusan Wildlife Reserve, both in the Barisan Mountains, ranked respectively as the sixth and eighth most effective protected areas for small felid habitat conservation in Sumatra. In the interior of Sumatra, we found that Air Sawan National Park and Dangku Wildlife Reserve were of considerable importance in terms of habitat for the felid species (ninth and tenth rank, respectively).

## Gap analysis

In mainland Southeast Asia, the largest unprotected area of medium and high habitat suitability for multiple small felid species occurred largely in Northern Myanmar, but extended also into the easternmost Indian states, Bangladesh, Bhutan and China (area A in Fig. 5; Table 4). Along the border between Myanmar and Thailand we identified the second largest suitable unprotected area, which extended across much of the two countries, but also included portions of Laos, China and Vietnam (area B). Adjacent to this area, we identified another area of high felid habitat suitability extending across the border between Laos and Vietnam (area D). In the northern parts of Vietnam, we found an additional unprotected area of suitable habitat for multiple felid species (area F). We also highlighted suitable areas in Southern Myanmar (area E), and in the southernmost extent of the Malay Peninsula, where we highlighted two adjacent areas across Malaysia and Thailand (areas C and I). We identified another highly important unprotected area for felid habitat in the Himalayan foothills of Bhutan (area G). In the Chinese province of Sichuan, we highlighted two smaller areas important for felid habitat suitability (areas H and J).

In Borneo, the largest area of unprotected high and medium suitability habitat extended across the central highlands of the Indonesian provinces of North, East and Central Kalimantan (area A in Fig. 6; Table 5). In Sabah, we highlighted the second largest suitable unprotected area (area B) and, adjacent to this one, we identified another area occurring in the eastern parts of Sabah (area E). Importantly, we mapped an unprotected area between the central highlands and Sabah playing a crucial role connecting these two strongholds

**Table 2** Main protected areas in terms of extent of high suitability habitat for the sampled felid species in Borneo

| Protected areas | Code | Low suitability habitat ($km^2$) | Low suitability habitat (%) | Medium suitability habitat ($km^2$) | Medium suitability habitat (%) | High suitability habitat ($km^2$) | High suitability habitat (%) |
|---|---|---|---|---|---|---|---|
| Sebangau | 1 | 443.81 | 0.39 | 1274.38 | 1.12 | 3784.88 | 7.11 |
| Bukit Baka—Bukit Raya | 2 | 18.94 | 0.02 | 69.31 | 0.06 | 1625.50 | 3.05 |
| Bukit Sapat Hawung | 3 | 0.00 | 0.00 | 67.94 | 0.06 | 1491.06 | 2.80 |
| Crocker Range National Park | 4 | 2.25 | 0.00 | 26.31 | 0.02 | 1367.75 | 2.57 |
| Kutai | 5 | 233.06 | 0.20 | 505.81 | 0.45 | 1096.44 | 2.06 |
| Tabin Wildlife Reserve | 6 | 4.56 | 0.00 | 155.88 | 0.14 | 955.44 | 1.79 |
| Kayan Mentarang | 7 | 0.81 | 0.00 | 32.94 | 0.03 | 840.94 | 1.58 |
| Kinabalu Park | 8 | 3.44 | 0.00 | 51.38 | 0.05 | 781.50 | 1.47 |
| Gunung Nyiut Penrissen | 9 | 31.56 | 0.03 | 167.69 | 0.15 | 711.75 | 1.34 |
| Gunung Palung | 10 | 93.13 | 0.08 | 231.44 | 0.20 | 704.81 | 1.32 |

Reported are the extent of the low, medium and high suitability habitats occurring in each protected area, and the proportion of the extent of the suitability class over the extent of that class in Borneo

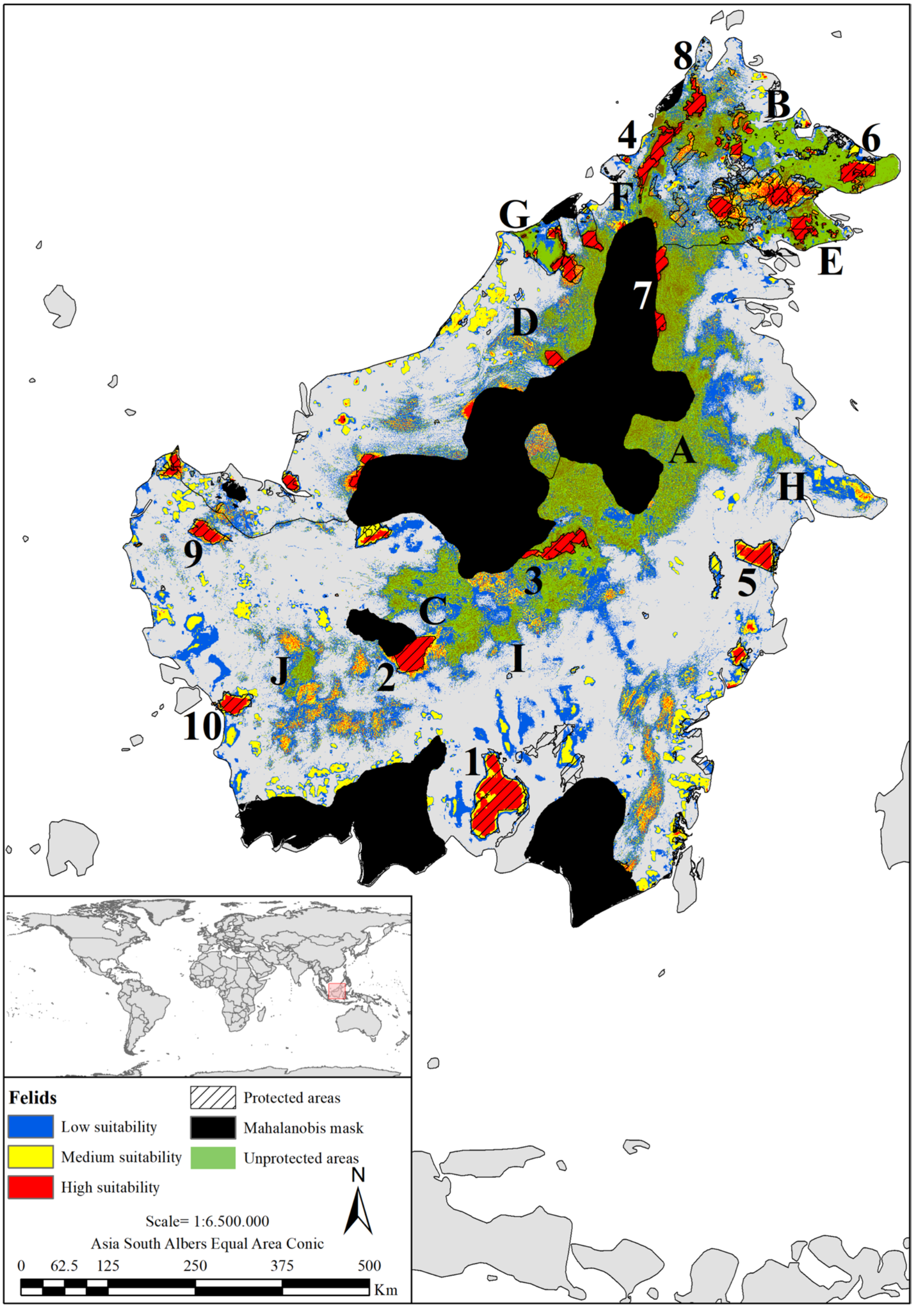


**Fig. 6** Reclassified probability surface of the sampled felid species in Borneo, showing areas with low, medium and high habitat suitability. Codes of the protected areas and of the unprotected suitable areas are reported in Tables 2 and 5, respectively

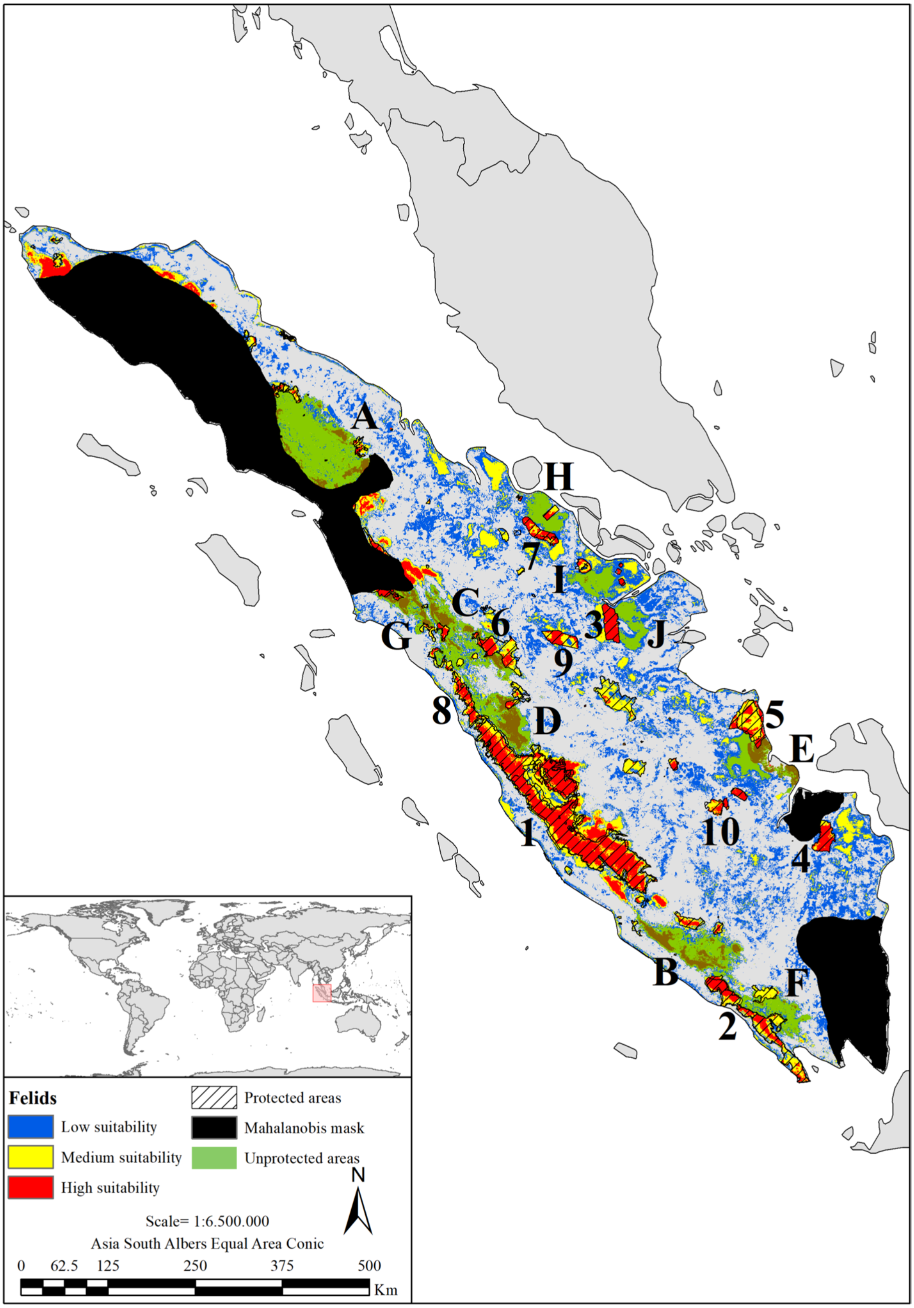


**Fig. 7** Reclassified probability surface of the sampled felid species in Sumatra, showing areas with low, medium and high habitat suitability. Codes of the protected areas and of the unprotected suitable areas are reported in Tables 3 and 6, respectively

**Table 3** Main protected areas in terms of extent of high suitability habitat for the sampled felid species in Sumatra

| Protected areas | Code | Low suitability habitat (Km$^2$) | Low suitability habitat (%) | Medium suitability habitat (Km$^2$) | Medium suitability habitat (%) | High suitability habitat (Km$^2$) | High suitability habitat (%) |
|---|---|---|---|---|---|---|---|
| Kerinci Seblat | 1 | 246.69 | 0.36 | 3340.13 | 5.40 | 9753.06 | 32.58 |
| Bukit Barisan Selatan | 2 | 166.88 | 0.24 | 1463.38 | 2.36 | 1406.00 | 4.70 |
| Kerumutan | 3 | 0.50 | 0.00 | 37.00 | 0.06 | 909.06 | 3.04 |
| Padang Sugihan | 4 | 0.88 | 0.00 | 167.38 | 0.27 | 680.06 | 2.27 |
| Berbak | 5 | 0.31 | 0.00 | 1080.56 | 1.75 | 643.50 | 2.15 |
| Bukit Rimbang Bukit Baling | 6 | 120.44 | 0.17 | 642.50 | 1.04 | 602.88 | 2.01 |
| Giam Siak Kecil | 7 | 0.50 | 0.00 | 205.81 | 0.33 | 576.31 | 1.93 |
| Arau Hilir dan Air Terusan | 8 | 22.06 | 0.03 | 340.94 | 0.55 | 536.31 | 1.79 |
| Air Sawan | 9 | 54.94 | 0.08 | 331.38 | 0.54 | 429.81 | 1.44 |
| Dangku | 10 | 0.69 | 0.00 | 204.75 | 0.33 | 241.75 | 0.81 |

Reported are the extent of the low, medium and high suitability habitats occurring in each protected area, and the proportion of the extent of the suitability class over the extent of that class in Sumatra

**Table 4** Largest unprotected suitable areas for the sampled felid species in mainland Southeast Asia, including medium and high suitability habitats

| Code | Country | Area ($km^2$) |
|---|---|---|
| A | Bangladesh, Bhutan, China, India, Myanmar | 289,168.00 |
| B | China, Laos, Myanmar, Thailand, Vietnam | 192,444.06 |
| C | Malaysia, Thailand | 49,414.38 |
| D | Cambodia, Laos, Vietnam | 43,892.63 |
| E | Myanmar, Thailand | 42,650.38 |
| F | China, Vietnam | 18,395.50 |
| G | Bhutan, China, India, Nepal | 13,684.19 |
| H | China | 7198.88 |
| I | Malaysia | 6559.31 |
| J | China | 6332.38 |

Codes refer to the ten largest unprotected suitable areas displayed in Fig. 5

**Table 5** Largest unprotected suitable areas for the sampled felid species in Borneo, including medium and high suitability habitats

| Code | Area ($km^2$) |
|---|---|
| A | 39,547.81 |
| B | 14,983.38 |
| C | 7511.06 |
| D | 6461.69 |
| E | 3100.25 |
| F | 2693.06 |
| G | 1819.81 |
| H | 1507.44 |
| I | 1182.94 |
| J | 1173.81 |

Codes refer to the ten largest unprotected suitable areas displayed in Fig. 6

(area F). South of the region excluded by the Mahalanobis mask, we identified two large areas of high quality unprotected smaller felid habitat in Central and West Kalimantan (areas C and I). Additionally, in the Malaysian state of Sarawak we highlighted an important unprotected area of highly suitable felid habitat (area D). We also mapped an important unprotected area for felid conservation extending within the borders of Brunei Darussalam (area G). Additionally, we highlighted suitable areas occurring in East Kalimantan (area H) and West Kalimantan (area J).

In Sumatra, the largest unprotected area of suitable small felid habitat covered a large portion of the mountainous parts of North Sumatra (area A in Fig. 7; Table 6), while the second largest suitable unprotected area was identified in the Southern Barisan Mountains, connecting Kerinci Seblat and Bukit Barisan Selatan National Parks (area B). Additionally, we highlighted another area of highly important unprotected felid habitat extending outwards from Bukit Barisan Selatan National Park (area F). Similarly, we found a suitable unprotected area contiguous with Kerinci Seblat National Park (area D). In the Barisan Mountains, we highlighted two additional areas (areas C and G). We identified unprotected suitable areas also in Eastern Sumatra, in close proximity with several protected areas.

**Table 6** Largest unprotected suitable areas for the sampled felid species in Sumatra, including medium and high suitability habitats

| Code | Area ($km^2$) |
|---|---|
| A | 10,274.38 |
| B | 4952.38 |
| C | 4435.88 |
| D | 3511.38 |
| E | 3013.75 |
| F | 2308.25 |
| G | 1737.38 |
| H | 1666.94 |
| I | 1651.00 |
| J | 1639.56 |

Codes refer to the ten largest unprotected suitable areas displayed in Fig. 7

Specifically, we mapped an area of suitable felid habitat surrounding Giam Siak Kecil Wildlife Reserve (area H), and two suitable areas adjacent to Kerumutan Wildlife Reserve (areas I and J). We also found suitable unprotected habitat adjacent to Berbak National Park (area E).

## Felids as biodiversity indicators

The assessment of the role of smaller felids as biodiversity indicators revealed that the smaller felid species associated with forest environments were generally strong indicators of broader biodiversity, and the stronger their forest association the stronger their indicator ability (e.g., clouded leopard, marbled cat, golden cat). Conversely, smaller felids that are associated with anthropogenically modified and nonforest habitat (leopard cat) were very poor indicators of broader biodiversity. The multi-species predictive layers for sampled felids together showed, overall, higher Pearson's correlation coefficients with previously published (Macdonald et al. 2020; Chiaverini et al. 2022) broader biodiversity maps in the region than the single-species habitat suitability layers (Tables 7, 8, 9). For example, for both Borneo and Sumatra the multispecies felid habitat suitability layer had higher correlation to regional biodiversity than did any individual species, while on the mainland the

**Table 7** Pearson's correlation coefficients of the single-species habitat suitability models and of the predictive surface of the sampled felids altogether, with the layer of vertebrate terrestrial biodiversity in mainland Southeast Asia

| | Clouded leopard | Asiatic golden cat | Marbled cat | Leopard cat | All felids |
|---|---|---|---|---|---|
| Biodiversity | 0.30 | 0.36 | 0.25 | −0.06 | 0.31 |

**Table 8** Pearson's correlation coefficients of the single-species habitat suitability models and of the predictive surface of the sampled felids altogether, with the layer of vertebrate terrestrial biodiversity in Borneo

| | Sunda clouded leopard | Borneo bay cat | Marbled cat | Sunda leopard cat | All felids |
|---|---|---|---|---|---|
| Biodiversity | 0.37 | 0.33 | 0.31 | 0.26 | 0.44 |

**Table 9** Pearson's correlation coefficients of the single-species habitat suitability models and of the predictive surface of the sampled felids altogether, with the layer of vertebrate terrestrial biodiversity in Sumatra

| | Sunda clouded leopard | Asiatic golden cat | Marbled cat | Sunda leopard cat | All felids |
|---|---|---|---|---|---|
| Biodiversity | 0.33 | 0.50 | 0.51 | 0.04 | 0.55 |

multispecies felid layer was ranked second in the strength of its correlation with regional predicted biodiversity patterns (after Asiatic golden cat).

In all cases leopard cat was the species with the lowest correlation with predicted regional biodiversity, with values near zero for the mainland and Sumatra, indicating its association with disturbed habitats that often have low remaining biodiversity levels. The other species were generally similar in having moderate to high correlations with regional predicted biodiversity (between 0.25 and 0.51).

## Discussion

This is the first assessment of the habitat suitability, protected area effectiveness and gap analysis for smaller felids replicated across three subregions of Southeast Asia. We identified the most suitable areas for small felids, assessed the effectiveness of protected areas in preserving highly suitable habitat for the species, and highlighted the most suitable areas still lacking formal protection. Finally, we evaluated the effectiveness of smaller felids as indicator species of regional biodiversity. Our results provide important information on the multispecies patterns of habitat quality and its degree of protection for small felids across Southeast Asia, which have rarely been the focus of conservation actions (Brodie 2009; Macdonald et al. 2015), despite their ecological importance (Chiaverini et al. 2022; de Oliveira et al. 2010) and potential ambassadorial role (Macdonald et al. 2017). Specifically, we found that the additive combination of habitat suitability across multiple felid species had a high correlation with predictions over overall biodiversity, and higher correlation than any individual species had. This suggests that areas that are suitable for multiple felid species have characteristics that also support high biodiversity overall. Thus, the felid guild as a whole is an indicator of biodiversity, more than is the occurrence of any one felid species.

### Mainland Southeast Asia

Our analysis of protected area effectiveness for small felid conservation on mainland Southeast Asia highlighted the importance of the Northern Forest Complex of Myanmar, which is a vast system of contiguous forests extending from Northern Myanmar across the border with Laos, China and India. This area is characterised by extensive contiguous forests and wide altitudinal range. The topographic heterogeneity along the altitudinal gradient in this region enhances environmental variety, promoting niche diversity that supports the coexistence of several potential competitors in a relatively small area (Macdonald et al. 2020; Wikramanayake 2002). As a result, Macdonald et al. (2020) found the Northern Forest Complex to be crucial also for the overall vertebrate terrestrial biodiversity. It was also identified as the most important node in the regional habitat and connectivity network for clouded leopard (Kaszta et al. 2020b).

Despite its immense importance to regional biodiversity conservation, the Northern Forest Complex is under a large and likely growing threat from development. Kaszta et al. (2020a) highlighted the critical threats to forest habitat in Northern Myanmar presented by the Belt and Road Initiative (Yu 2017) and other regional developments, even before recent political developments in Myanmar that seem likely to lessen attention to biodiversity conservation there. Our results clearly emphasize that Northern Myanmar and adjacent areas of neighbouring countries contain the largest area of highly suitable habitat currently lacking protection in the entire region.

We identified another stronghold of multispecies suitability for small felids in Eastern Myanmar, extending across most of Laos and southwards towards the Malay Peninsula. This region was only partially highlighted as a biodiversity hotspot by Macdonald et al. (2020), and differences between that more broadly based analysis and our current research focused on small felids were particularly evident in Northern Laos. Kaszta et al. (2020a), however, in an assessment of core and corridors for mainland clouded leopard, also identified this region as a highly important extensive core habitat area for that species.

Along the border between Laos and Vietnam we found some of the most important protected areas in mainland Southeast Asia, based on habitat potential for small felids. These promising results for small felids in Laos and Vietnam come in the wider context of the extirpation of tigers (*Panthera tigris*) and leopards (*Panthera pardus*) from Northern Laos (Rasphone et al. 2019) and all of Vietnam. If the rampant snaring in this region is not staunched, other species will soon follow (Johnson et al. 2016). Indeed, all small felids except leopard cat are likely already extirpated from Vietnam (Willcox et al. 2014), and clouded leopard, marbled cat and leopard cat appear to be rapidly declining in Northern Laos' largest and best protected area (Rasphone et al. 2021). Therefore, the snaring crises in Southeast Asia does not bode well for the future of small felids, despite favourable habitat still occurring in the region. Additionally, and as in Northern Myanmar, the Belt and Road Initiative is likely to impact biodiversity negatively also in Northern Laos (Ng et al. 2020).

Landscapes degraded by intense agricultural activities were a major limit to the extensiveness of suitable habitat for small felids in Cambodia, where the only suitable areas remained in the protected areas on the northern border with Laos and in the Cardamom Mountains. However, previous work has shown that preserving dry deciduous forests in Eastern Cambodia is critical for conserving jungle cat (*Felis chaus*), a specialist of these habitats (Rostro-Garcia et al. 2021). Although we identified suitable habitats for smaller felids in Cambodian protected areas, biodiversity in the country is critically threatened by hunting and snaring (Harrison et al. 2016).

In Thailand, the negative effects of land degradation were particularly evident: along the northern portion of the Malay Peninsula, the boundary between suitable and unsuitable habitats could be traced along the border with Myanmar. On the Myanmar side of that border, we identified both protected and unprotected suitable habitats in forested areas along the peninsular extent of the country, while on the Thai side little suitable habitat was identified.

### Borneo

In Borneo, we highlighted the critical role of protected areas for small felids, given that we found that one-quarter of highly suitable habitat was encompassed within the ten most effective protected areas. This result was unexpected, since Chiaverini et al. (2022) found that less than 10% of Bornean terrestrial biodiversity was encompassed within protected areas. This difference suggests that small felids may depend more heavily on protected areas than does broader cross-taxa biodiversity. Chiaverini et al. (2022) found the highest numbers of vertebrate terrestrial species in the Malaysian state of Sabah, in the north of the island, while our analysis shows that the largest and most suitable habitat for small felids occurred in the central highlands of Borneo. This area is less impacted by forest loss than the surrounding regions (Cushman et al. 2017). It represents a vital refuge for felids, and for other specialised species, compared to the more disturbed lowlands (Scriven et al. 2015). Importantly, this region overlapped with the Heart of Borneo initiative, a transboundary conservation area signed between Brunei Darussalam, Indonesia and Malaysia to manage the last undisturbed forests of the island (Keong and Onuma 2021). In the central highlands our modelled distribution for small felids matched the Heart of Borneo's proposed outline, but extended beyond it. Extending from the Heart of Borneo, we modelled suitable habitats in the mountainous region along the Mangkalihat Peninsula in East Kalimantan, along the range of the Meratus Mountains in South Kalimantan, and in West and Central Kalimantan. In these regions, we highlighted scattered unprotected suitable areas, but also the most important protected areas in Borneo.

The proposed new Indonesian capital of Nusantara is being built in Southeast Borneo. This new global megacity is certain to have large impacts on biodiversity. Kaszta et al. (2024) evaluated the potential impacts of this new city on clouded leopard habitat quality and connectivity. This paper shows that several other small felid species, notably marbled cat, have high predicted habitat quality in the region of the new capital and may also be highly impacted by its development.

Additionally, our analysis shows that the northernmost extent of Sabah contains expansive suitable habitat for small felids both within and outside protected areas. Although the carnivore distribution maps produced by Mathai et al. (2016) differed from our prediction in this area, our predictions corresponded to those produced by Hearn et al. (2018) for several small and midsized felids. Consistent with our identification of Northern Sabah as an important region for small felid habitat, Chiaverini et al. (2022) also found this area to be a hotspot for Bornean terrestrial biodiversity.

## Sumatra

In Sumatra, we highlighted the overwhelming importance of the Barisan Mountains, extending along the western coastal region, and representing the stronghold of suitability for small felids. Our predicted multi-species suitability for small felids closely matched the modelled habitat suitability for Sunda clouded leopard on the island (Macdonald et al. 2018). Although the entire mountain range harboured suitable habitats, the most suitable areas largely corresponded with Kerinci Seblat and Bukit Barisan Selatan National Parks, two of the largest protected areas in Sumatra. Notably, both these areas are part of the Tropical Rainforest Heritage of Sumatra, a UNESCO World Heritage site that includes also Gunung Leuser National Park, occurring in the northern parts of the island that were almost entirely excluded by the Mahalanobis mask. Importantly, along the Barisan Mountains we also mapped extensive regions of suitable but unprotected areas, often occurring in close association with the most important protected areas.

In the eastern regions of Sumatra we also identified highly suitable habitats in association with protected areas, mirroring the findings of Chiaverini et al. (2022) for terrestrial vertebrate biodiversity. The eastern provinces of Sumatra are among the most affected by deforestation for oil palm and wood fibre plantations (Singh and Yan 2021), and protected areas likely represent the only remaining refuge for small felids in this region, except for leopard cat, which has higher tolerance for disturbed ecosystems (Mohamed et al. 2013). Importantly, we found suitable unprotected areas in close association with most of the main protected areas in Eastern Sumatra as well. These areas are notable candidates for additional protection, with the capacity to buffer existing protected areas from deforestation and land degradation (Singh and Yan 2021).

## Conclusions

Our analysis used scale-optimized habitat suitability models for three regions of Southeast Asia for several species of smaller felids to map multispecies habitat suitability, assess the effectiveness of the existing protected area network for small felids, identify important areas of unprotected small felid habitat and assess the ability of small felids to indicate patterns of wider biodiversity. Overall, we believe this paper provides several urgently needed and timely evaluations. It is essential to assess the current multispecies patterns of habitat quality using large empirical datasets collected in situ and analysed with rigorous modelling tools. Our analysis provides the first region-wide, multispecies assessment, mapping and prioritization of areas for small felid conservation. We identified several regions in the mainland, on Borneo and on Sumatra where remaining habitat for multiple small felid species is concentrated. We identified and ranked the effectiveness of existing protected areas in each subregion and mapped the most important areas in each that still contain unprotected high quality habitat for multiple felid species. These results are highly consistent with previous work on single species (e.g., Macdonald et al. 2019, 2020; Kaszta et al. 2020a) and with broader patterns of regional biodiversity (e.g. Macdonald et al. 2020; Chiaverini et al. 2022). Collectively, our results, and the previous studies they corroborate, are a clarion call for focused efforts to expand the extent, and improve the conservation management, of protected areas in the remaining core habitat areas for multiple species in Southeast Asia, and to work to enhance and protect connectivity between them to ensure long-term demographic and genetic exchange among the region's remaining wildlife populations (e.g., Kaszta et al. 2020a).

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**Author contributions** LC and SAC conceptualised the ideas and designed the methodology. DWM conceived the larger framework on which the study is based and secured the funding. AJH, EA, ÖEC, PC, SMC, GRC, IAH, JFK, PPK, MSL, AR, PS, CKWT and BPY managed and coordinated individual field teams that collected the data. LC analysed the data with substantial contribution of SAC. LC, with substantial contribution of SAC, DWM, AJH and ŻK interpreted the results. LC led the writing, with substantial contribution of SAC, DWM, AJH and ŻK. All authors contributed critically to the drafts and gave final approval for publication.

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**Data availability** Given the extremely sensitive nature of species occurrence data with respect to illegal wildlife trade, locations of camera traps will not be made public to avoid further endangering the already threatened species. However, we welcome correspondence with scholars and conservationists regarding collaborative use of the data to advance science and conservation of Southeast Asian felid species. No datasets were generated or analysed during the current study.

## Declarations

**Competing interests** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



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