



Identifying conservation priorities for an understudied species in decline: Golden cats (*Catopuma temminckii*) in mainland Tropical Asia

Wyatt Joseph Petersen^{a,*}, Tommaso Savini^a, Thomas N.E. Gray^{b,c}, Megan Baker-Whatton^d, Francesco Bisi^{e,f}, Wanlop Chutipong^a, Giacomo Cremonesi^e, George A. Gale^a, Shariff Wan Mohamad^g, D. Mark Rayan^h, Naret Seuaturienⁱ, Nay Myo Shwe^j, Kittiwara Siripattaranukul^k, Kriangsak Sribuarod^l, Robert Steinmetzⁱ, Niti Sukumal^a, Dusit Ngoprasert^a

^a Conservation Ecology Program, King Mongkut's University of Technology Thonburi, 49 Thakham, Bangkhuntien, Bangkok 10150, Thailand

^b Wildlife Alliance, 86, St 123, Toultompong I, Phnom Penh, Cambodia

^c WWF Tigers Alive Initiative, Phnom Penh, Cambodia

^d The Nature Conservancy, 4245 Fairfax Drive, Arlington, VA 22203, USA

^e Environment Analysis and Management Unit - Guido Tosi Research Group – Department of Theoretical and Applied Sciences, University of Insubria, Via J. H. Dunant, 3, I-21100 Varese, Italy

^f Istituto Oikos Onlus, Via Crescenzago 1, 20134 Milano, Italy

^g WWF-Malaysia, 1 Jalan PJS 5/28A, Petaling Jaya Commercial Centre, 46150 Petaling Jaya, Selangor, Malaysia

^h Wildlife Conservation Society-Malaysia, 42-C, 3rd Floor, Jalan SS6/8, Kelana Jaya, 47301 Petaling Jaya, Selangor, Malaysia

ⁱ WWF-Thailand, Pisit Building, 11 Pradiphat Soi, 10 Pradiphat Road, Phayathai, Bangkok 10400, Thailand

^j Fauna & Flora International, Myanmar Program, Yangon, Myanmar

^k Forest Biology Department, Faculty of Forestry, Kasetsart University, 50 Phahonyothin road, Chatuchak District, Bangkok 10900, Thailand

^l Khlong Saeng Wildlife Research Station, Department of National Park, Wildlife and Plant Conservation, Paholyotin Road, Chatuchak, Bangkok 10110, Thailand

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ABSTRACT

Identifying conservation priorities for an understudied species can be challenging, as the amount and type of data available to work with are often limited. Here, we demonstrate a flexible workflow for identifying priorities for such data-limited species, focusing on the little-studied Asian golden cat (*Catopuma temminckii*) in mainland Tropical Asia. Using recent occurrence records, we modeled the golden cat's expected area of occurrence and identified remaining habitat strongholds (i.e., large intact areas with moderate-to-high expected occurrence). We then classified these strongholds by recent camera-trap survey status (from a literature review) and near-future threat status (based on publicly available forest loss projections and Bayesian Belief Network derived estimates of hunting-induced extirpation risk) to identify conservation priorities. Finally, we projected the species' expected area of occurrence in the year 2000, approximately three generations prior to today, to define past declines and better evaluate the species' current conservation status. Lower levels of hunting-induced extirpation risk and higher levels of closed-canopy forest cover were the strongest predictors of recent camera-trap records. Our projections suggest a 68% decline in area with moderate-to-high expected occurrence between 2000 and

* Corresponding author.

E-mail address: mail@wyattpetersen.com (W.J. Petersen).

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2020, with a further 18% decline predicted over the next 20 years. Past and near-future declines were primarily driven by cumulatively increasing levels of hunting-induced extirpation risk, suggesting assessments of conservation status based solely on declines in habitat may underestimate actual population declines. Of the 40 remaining habitat strongholds, 77.5% were seriously threatened by forest loss and hunting. Only 52% of threatened strongholds had at least one site surveyed, compared to 100% of low-to-moderate threat strongholds, thus highlighting an important knowledge gap concerning the species' current distribution and population status. Our results suggest the golden cat has experienced, and will likely continue to experience, considerable population declines and should be considered for up-listing to a threatened category (i.e., VU/EN) under criteria A2c of the IUCN Red List.

1. Introduction

Assessing and updating the conservation status of a threatened species is crucial for setting conservation priorities and guiding management strategies. Maintaining up-to-date species distribution maps, identifying and delineating threats, tracking past changes in area of occupancy, and predicting future changes in area of occupancy, are just a few aspects of this process (e.g., Guisan et al., 2006; Foden et al., 2019; Politi et al., 2020). However, consequential and timely assessments of conservation status can be challenging for understudied species, as the distributions of such species and their threats are often incompletely known, out-of-date, or unknown (e.g., Li et al., 2016). Under circumstances of limited data, an accessible, straightforward, and flexible workflow that enables stakeholders to incorporate available data may prove useful during assessments, thereby aiding in the identification of conservation priorities and the development of successful management strategies.

The Asian golden cat (*Catopuma temminckii*, “golden cat”) is an understudied felid native to the forests of mainland and insular Tropical Asia (McCarthy et al., 2015). Currently, the species has been assessed as Near Threatened by the International Union for the Conservation of Nature (IUCN) Red List, citing potential past, present, and future population declines and range contractions (McCarthy et al., 2015). However, accurately assessing this species' conservation status has proven difficult as few focused studies on golden cats have been undertaken (McCarthy et al., 2015; Zanin et al., 2015). This inability to assess the species' status accurately is problematic, as evidence from previous reviews (e.g., Willcox et al., 2014; McCarthy et al., 2015) suggest golden cats may already be extirpated (or functionally so) across extensive areas of their historic range; particularly in mainland Tropical Asia where indiscriminate wildlife poaching, both for trade and subsistence, has occurred at unsustainable levels for years (McCarthy et al., 2015; Harrison et al., 2016; Gray et al., 2018). Indeed, golden cat records from Cambodia, China, Laos, and Vietnam have all drastically decreased over the past two decades, with declines attributed to elevated poaching levels in these countries (Willcox et al., 2014; McCarthy et al., 2015). Considering these potential declines, there is an urgent need to re-assess the species' conservation status and identify priorities for future conservation efforts, especially across mainland Tropical Asia where declines appear to be greatest. An up-to-date delineation of expected golden cat occurrence in mainland Tropical Asia, especially one that incorporates potential impacts from threats such as poaching, as well as a subsequent assessment of past and likely future declines, and an identification of priority areas, would mark an important first step towards such an endeavor and may prove useful as a case-study for species faced with a similar predicament.

The aim of this paper was to improve our understanding of the conservation status of, and set priorities for, the little-studied and possibly threatened golden cat in mainland Tropical Asia; and in the process demonstrate a straightforward workflow applicable to similar species. First, we delineate the remaining habitat where golden cats are expected to occur based on recent occurrence records, current forest cover, and a proxy for hunting threat. We then identify large contiguous areas with moderate-to-high expectation of occurrence (‘strongholds’) and classify these areas by survey status, based on the results of a literature review for recent camera-trap surveys (2010–2020), and threat, based on predicted declines in stronghold areas in the near future (2020–2040), to facilitate the prioritization of future conservation and research efforts. Finally, we estimate expected golden cat occurrence in 2000, approximately three generations before 2020 (Pacifiçi et al., 2013), to define past declines and better evaluate the species' current conservation status within the framework of an IUCN Red List assessment.

2. Methods

2.1. Study site

The study was conducted over the golden cat's historical mainland range, comprising the mainland parts of Southeast Asia, southern China, northeastern India, Bangladesh, and the eastern Himalayas (McCarthy et al., 2015).

2.2. Species record locations

We compiled 312 recent (2010–2020) presence-only points from multiple sources across 11 countries spanning the golden cat's known mainland range. Presence-only points were sourced from direct contributions provided by collaborators (189 points) and from the literature (123 points). We conducted our literature search on Google Scholar, Semantic Scholar, and Web of Science Core Collection, searching for evidence of recent golden cat records and recent camera-trap surveys (trap-nights \geq 500; following Petersen

et al., 2020) within the golden cat's known range. We also searched the gray literature, including unpublished graduate student theses, internal reports from conservation-focused government departments and non-governmental organizations, internet-based biodiversity databases (i.e., gbif.org, inaturalist.org, emammal.si.edu), and social media (e.g., Facebook, Weibo) when available. To reduce the potential for spatial-autocorrelation among points and reduce variability in sampling intensity among landscapes, we filtered all

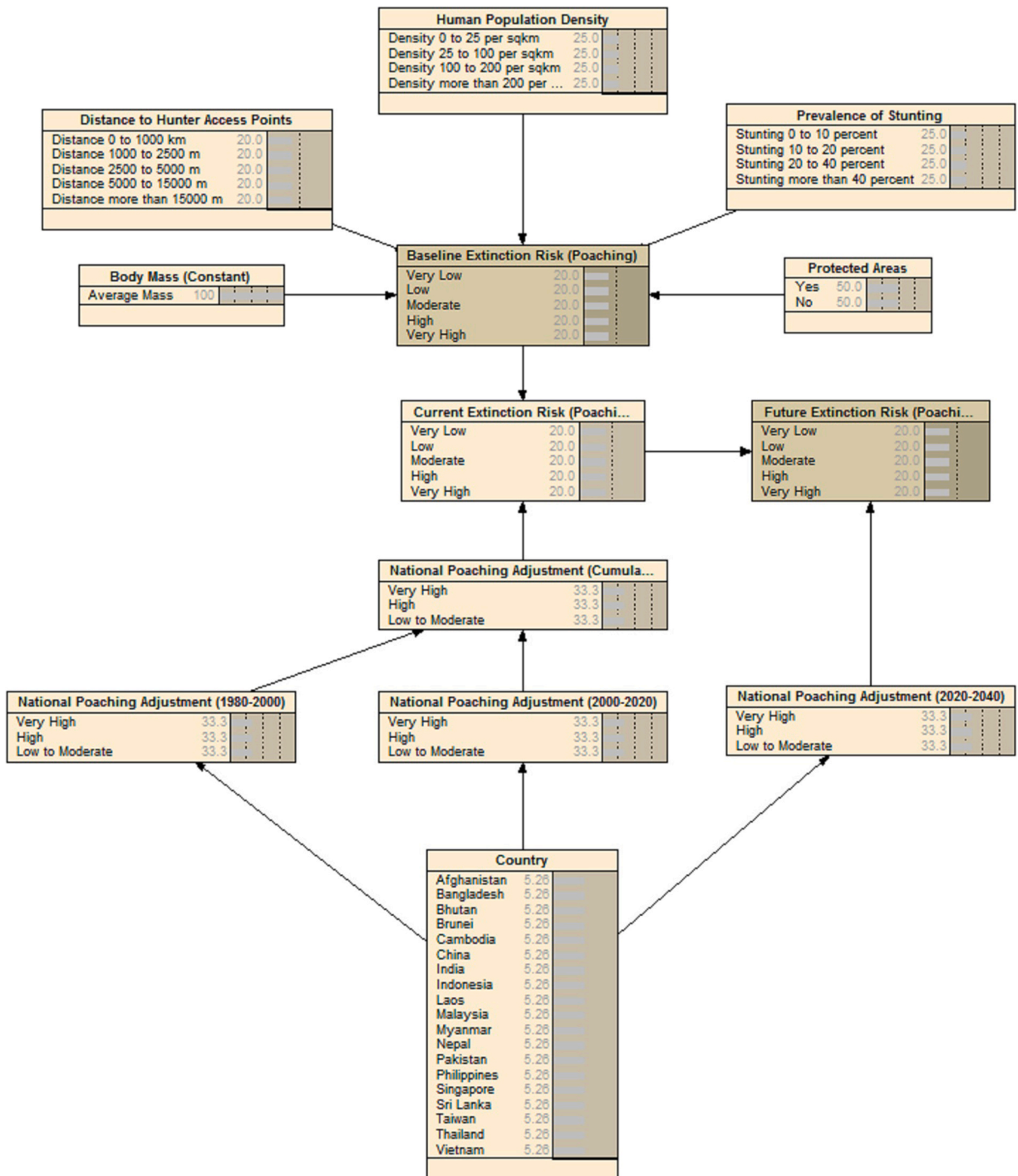


Fig. 1. Bayesian Belief Network used to predict hunting induced extirpation risk facing Asian golden cats (*Catopuma temminckii*) in mainland Southeast Asia. Baseline extirpation risk was based on the pan-tropical findings of Benítez-López et al. (2019). Expert opinion was used to adjust the baseline risk to accommodate variation in potential hunting intensity between range countries and time periods (1980–2000, 2000–2020, and 2020–2040).

presence-only points by 6 km using the “thin” function in the R 4.0.2 (R Development Core Team, 2020) package ‘spThin’ 0.2.0 (Aiello-Lammens et al., 2019), leaving 106 points for final analysis. A filter size of 6 km represents the approximate diameter of a female golden cat’s home-range, based on the conversion of an available telemetry-based home range estimate (33 km²; Grassman et al., 2005) to a circular home range expected to contain 95% of activity (Royle et al., 2014).

2.3. Delineating hunting-induced extirpation risk

We used a Bayesian Belief Network to delineate relative hunting-induced extirpation risk facing golden cats and other medium-to-large bodied mammals (>1 kg) following Petersen et al. (2020; Fig. 1). Bayesian Belief Networks are probabilistic graphical models that represent conditional dependencies (indicated by directed arrows known as “arcs”) between variables of interest (“nodes”). Conditional dependencies are provided in the form of probability tables and underlie the relationship between “child” nodes and the “parent” nodes that child nodes depend on (e.g., “Human Population Density” and “Distance to Hunter Access Points” are both parent nodes to “Baseline Extinction Risk”, Fig. 1). Specifically, each child node is associated with a conditional probability function that takes, as input, a particular set of values from the child node’s “parents”, and gives, as output, the probabilities of each of the child node’s potential states (e.g., “Baseline Extinction Risk” has five potential states: very low, low, moderate, high, and very high; Fig. 1). The results of our network’s “Current Extinction Risk” node represent the final output of our model and were used to construct a relative hunting-induced extirpation risk map for 2020.

“Current Extinction Risk” was conditional on both local and national factors. We defined baseline (local) risk using five factors likely to predict hunting-induced mammal defaunation in the tropics (Benítez-López et al., 2019). These factors were distance to hunter access points (i.e., human settlements), human population density, protected area status, species body mass, and the proportion of young children (age < 5 years) facing chronic malnourishment (“stunting”). However, for our study, we revised the original definition of hunter access points used by Benítez-López et al. (2019) to include additional indicators of human presence (i.e., human settlements, roads, buildings, nightlights, and anomalous forest loss clusters; see Appendix A1, A2, A3, A4, A5 for more details). Although the findings of Benítez-López et al. (2019) were not specific to golden cats, we do consider their general findings—which were based on a pan-tropical, multi-taxa assessment of mammal defaunation using a database of over 3,000 hunting-induced mammal abundance declines—to be broadly applicable to golden cats and, although not explicitly considered here, their potential prey. Besides the five factors identified by Benítez-López et al. (2019), evidence suggests general poaching intensity in Tropical Asia varies by nation and culture (e.g., Harrison et al., 2016). To account for some of these differences, we interviewed experts, asking them to rank range countries based on perceived past (1980–2000), present (2000–2020), and likely future (2020–2040) poaching intensity with respect to medium-to-large mammals (> 1 kg, including golden cats and potential prey). Experts (n = 6) were selected based on previous experience (≥ 10 years) working in the fields of wildlife ecology and conservation within Tropical Asia. For each period, experts ranked range countries as low, moderate, high, or very high poaching intensity relative to other countries. Local risk of hunting-induced extirpation was then adjusted higher for countries that ranked high or very high in any single period, with risk adjusted the highest for countries ranking high or very high over multiple consecutive periods. We provide all conditional probability tables and steps taken to run the analysis as supplementary material (Appendix A6).

2.4. Modeling recent (2010–2020) occurrence records

We used our spatially filtered presence-only data to model recent golden cat occurrence (2010–2020) across mainland Tropical Asia in relation to various environmental and anthropogenic predictor variables. A total of 12 predictor variables were a priori selected for modeling golden cat occurrence, including land-cover variables [percentage forest cover in 2019 (the most recent year available at time of writing), percentage closed-canopy (≥70% canopy cover) forest cover, percentage open-canopy (20–70% canopy cover) forest cover; derived from Hansen et al. (2013)], topographic variables (elevation and terrain roughness; Amatulli et al., 2020), climatic variables (annual mean temperature, mean temperature during the warmest/coldest quarters, annual precipitation, precipitation during the wettest/driest quarters; CHELSA, Karger et al., 2017), and anthropogenic variables (relative hunting-induced extirpation risk; see *Methods – Delineating hunting-induced extirpation risk*). We distinguished between closed-canopy and open-canopy forests because we considered this distinction to be ecologically relevant; and while a single continuous variable representing mean percentage canopy-cover would also have worked, it would risk conflating some human-dominated areas with forests that possess naturally low canopy cover (e.g., the agricultural edge of a closed-canopy evergreen forest in central Thailand might receive the same score as the core of an open-canopy deciduous forest in eastern Cambodia). To assess scalar relationships between golden cat occurrence data and the environment, we transformed each predictor variable into eight, multi-scale covariates following Macdonald et al. (2019), resulting in 96 total variables for analysis. Variables were transformed using the “Focal Statistics” tool in ArcGIS Pro 2.2.0 (Environmental Systems Research Institute, 2018), with circular neighborhood distances corresponding to each scale of interest (radius = 250 m, 500 m, 1 km, 2 km, 4 km, 8 km, 16 km, and 32 km). All variables were in raster format and standardized with 250 m resolution and Asia South Albers Equal Area Conic projection.

We constructed infinitely weighted logistic regression models (Hefley and Hooten, 2015), to investigate the relationship between recent golden cat occurrence data and various environmental and anthropogenic predictor variables. All statistical analyses were conducted in R, using the “glm” function, with weights of 1 assigned to presence points and weights of 10e⁶ assigned to background (‘pseudo-absence’) points. To generate a suitable mask for background locations, we first buffered the locations of all presence-points and the locations of any camera-trap survey with ≥ 500 trap-nights found during our literature review (whether golden cats were detected or not) by 32 km (the largest predictor scale investigated). We then clipped this mask by available habitat (i.e., so the mask

did not overlap bodies of water, intensive agriculture, or urban areas; Appendix B). 10,000 background points, based on the minimum needed to stabilize β coefficients in the best-fit model, were then generated from random sampling within this mask using the “randomPoints” function in R package ‘dismo’ 1.1–4 (Hijmans et al., 2017). The “extract” function in the R package ‘raster’ 3.3–13 (Hijmans, 2020) was used to extract the appropriate covariate values for each presence and background location. All covariates were standardized by subtracting the mean and dividing by one standard deviation (Gelman, 2008). Variables exhibiting a high degree of multicollinearity (Spearman’s $\rho \geq |0.7|$) were not allowed to occur together within the same model.

Past studies investigating the influence of spatial scale on species-habitat relationships have generally identified the best scale using univariate model selection (“pseudo-optimization” of spatial scales, *sensu* McGarigal et al., 2016; e.g., Macdonald et al., 2019; Ashrafzadeh et al., 2020). Specifically, “the investigator evaluate[s] each covariate separately across a range of pre-specified scales and uses statistical measures [e.g., AIC] to select the single best scale for each covariate, then combine[s] the covariates (at their best univariate scale) into a single multi-variable, multi-scale model” (McGarigal et al., 2016). However, one possible limitation of this approach is that optimal scales are not determined multivariately and thus there is the potential for investigators to overlook the possibility that a covariate’s optimal scale depends on the inclusion of other covariates in the model. However, addressing this issue can be computationally demanding due to the sheer number of multivariate scale combinations, a practical limitation that may explain why, during the course of their review of multi-scale habitat selection studies, McGarigal et al. (2016) found only two studies attempting to identify a variable’s best scale multivariately. In these instances, the studies used a numerical optimization algorithm to search their vast parameter state-space for the optimal multi-scale solution (McGarigal et al., 2016). Since our models were quick to run and not particularly resource intensive, we opted for a brute-force approach whereby we searched our entire parameter state-space for the optimal multi-scale solution. To do so, we relied on the ‘MuMin’ (v1.43.17; Bartoń, 2020) R package’s “dredge” function, and its ‘subset’ argument, to generate a model selection table for multiple possible variable and scale combinations (“model subsets”), thereby allowing us to empirically optimize scales in the presence of other variables. Our use of the subset argument allowed for the exclusion of highly correlated variables within the same model, as well as the exclusion of the same variable, but of different scales, within the same model. Akaike information criterion for small sample sizes (AIC_c) and AIC weights were used to select the best-performing model. Since infinitely weighted logistic regression results in unidentifiable intercepts (i.e., the intercept shrinks towards negative infinity as the number of background points, or their weighting, increases; Fithian and Hastie, 2013), we replaced the intercept of our final model with 0. Therefore, the model’s continuous predictions, although ranging from 0 to 1, should be treated as a relative measure of occurrence which we refer to as relative occurrence rates (ROR; *sensu* Merow and Silander, 2014) throughout the remainder of the text.

2.5. Projecting past occurrence (2000)

We used the results of our final regression model to estimate golden cat occurrence in 2000, approximately three generations prior to 2020 (Pacifci et al., 2013). Data used for this projection included closed-canopy ($\geq 70\%$ canopy cover) forest cover in 2000 (Appendix C6; Hansen et al., 2013), current annual precipitation (CHELSA, Karger et al., 2017), and past hunting-induced extirpation risk (Appendix C7). We predicted past hunting-induced extirpation risk using our Bayesian Belief Network (see *Methods – Delineating hunting-induced extirpation risk*) by replacing the human population density and protected areas covariates with same source versions representative of 2000 and by setting the model to ignore the current (2000–2020) and likely future (2020–2040) national poaching modifiers (Appendix A7, A8). However, prevalence of stunting and distance to hunter access points were unchanged as reliable data from 2000 was not available. While we recognize this to be a potential limitation, we do not consider it to be an egregious one. One recurring limitation of settlement or road-mapping (i.e., potential hunter-access points) efforts in Tropical Asia is that many “featureless” areas do in fact possess infrastructure (roads/settlements) that has not yet been mapped (e.g., Hughes, 2017). And while the road network in Tropical Asia has greatly improved and expanded over the last 20 years, many such changes represent improvements to existing infrastructure (e.g., trails and dirt tracts become paved roads, two-lane roads become four-lane highways, etc.). Thus, it is possible our current dataset more accurately maps the locations of potential access points in 2000 than a hypothetical older dataset.

2.6. Projecting near-future occurrence (2020–2040)

We investigated potential near-future changes in golden cat occurrence using three hypothetical threat scenarios: (1) increased forest loss and hunting pressure (“business-as-usual”), (2) increased forest loss only, and (3) increased hunting only. We created prediction maps for each future scenario using the results of our final regression model and a combination of current and hypothetical future forest cover and hunting-induced extirpation risk maps (Appendix C1, C2, C3, C4, C5). The business-as-usual scenario (1) incorporated a future closed-canopy forest cover map (Appendix C2) and a future hunting-induced extirpation risk map (Appendix C4). The forest-loss-only scenario (2) incorporated the same future closed-canopy forest cover map used in scenario 1 and the original (2020) hunting-induced extirpation risk map (Appendix C3). The hunting-only scenario (3) incorporated the original (2019) closed-canopy forest cover map (Appendix C1) and the same future hunting-induced extirpation risk map used in scenario 1. As we were interested in understanding the relative impact of near-term threats facing golden cats, we chose not to consider the potential effects of climate change in any scenario.

To calculate a hypothetical future hunting-induced extirpation risk map, we used the output from our Bayesian Belief Network’s “Future Extinction Risk” node, as opposed to the “Current Extinction Risk” node, to create a relative threat map based on the expert assessment of likely future poaching intensity (Fig. 1; see Section 2.3 for more details). To account for potential forest loss, we revised

our 2019 map of closed-canopy forest cover by removing forested areas that were identified in a recent global study (Hewston et al., 2019) as having a high potential for tree cover loss (probability > 0.5) by 2029 (approximately half-way between our near-future period). Hewston et al. (2019) used annual tree-loss data, spatially-explicit and globally-consistent variables, and a multi-layer perceptron neural network to analyze patterns of past tree-cover loss and to model future risks of tree-cover loss based on a business-as-usual scenario. The global map of tree-cover transition potential used here is licensed under a Creative Commons Attribution 4.0 International License and available freely online at <https://futureclimates.conservation.org/riskstreecoverloss.html> and <https://zenodo.org/record/3237796#.X5f5Elj7SUK>.

2.7. Validating past and present prediction maps

We used continuous Boyce indices to evaluate our 2000 and 2020 prediction maps. The continuous Boyce index is a threshold-independent presence-only method that measures the relationship between the predicted and expected number of validation points for different ROR values (Boyce et al., 2002; Hirzel et al., 2006). The method works by first partitioning a continuous prediction map into multiple classes (or bins) using a moving window and then calculates predicted and expected occurrence frequencies for each class (Manzoor et al., 2018). A predicted-to-expected ratio for each bin is then calculated (ratios > 1.0 indicate the bins are predicting more presences than expected by chance; ratios < 1.0 indicate the opposite) and the ratios are plotted in the form of a predicted-to-expected curve. A Spearman rank correlation test then evaluates if the predicted-to-expected curve significantly increases as ROR values increase. The resulting correlation coefficient represents the actual continuous Boyce index value and can vary between -1.0 and 1.0, like any other correlation coefficient, with values close to zero indicating the model's predictions are no different from a random model, negative values indicating predictions are worse than those from a random model, and positive values indicating predictions are better than those from a random model. We considered continuous Boyce index values between 0.7 and 0.9 to indicate good predictive accuracy and values > 0.9 to indicate very good predictive accuracy (Boyce et al., 2002; Hirzel et al., 2006). All continuous Boyce indices were calculated using the 'contBoyce' function in R package "enmSdm" (0.5.3.3; Smith, 2021).

We used two datasets to evaluate the predictive accuracy of our 2020 prediction map. These datasets included (1) our original training points (n = 106) and (2) an external test dataset consisting of georeferenced occurrence points from Bhutan (n = 228) that were published after our data collection phase was completed and thus not included in our original analyses (Penjor et al., 2021). A single external dataset was collated to evaluate the predictive accuracy of our 2000 prediction map. Owing to the limited number of published camera-trap surveys available for reference in 2000, we also included camera-trap records between 1995 and 2005 and other forms of published records (i.e., direct sightings and interview surveys). Out of 599 locations georeferenced across seven countries (Cambodia, China, Laos, Malaysia, Myanmar, Thailand, Vietnam), only 62 had golden cat detections (Appendix E1).

2.8. Identifying past, present, and future habitat strongholds

We identified potential habitat strongholds in 2000, 2020, and 2020–2040 using each period's respective prediction maps. To do so, we reclassified our continuous prediction maps into categories of expected occurrence based on the minimum training presence threshold (Pearson et al., 2007), predicted-to-expected ratio, and predicted-to-expected curve from our continuous Boyce index (using our 2020 prediction map and training data; see Section 2.7), following Hirzel et al. (2006). First, using the predicted-to-expected ratio, we defined two initial classes of expectation: low expectation of occurrence (i.e., predicted-to-expected ratios ≤ 1.0) and moderate-to-high expectation of occurrence (i.e., predicted-to-expected ratios > 1.0). Second, using our minimum training presence threshold, we subdivided our low expectation of occurrence class into very low (i.e., values below our minimum training presence threshold) and low (i.e., values above our minimum training presence threshold) expectation of occurrence sub-classes. Finally, using trends in our predicted-to-expected curve, we subdivided our initial moderate-to-high class of expectation into three sub-classes: moderate (i.e., a predicted-to-expected ratio ca. 1.0–5.0), high (i.e., a predicted-to-expected ratio ca. 5.0–15.0), and very high (i.e., a predicted-to-expected ratio > 15.0). For consistency, we reclassified our past (2000) and near-future (2020–2040) prediction maps using the same thresholds as our 2020 prediction map. We then defined habitat strongholds as being large contiguous areas ($\geq 1,000 \text{ km}^2$) with moderate-to-high expectation of occurrence (i.e., areas with predicted-to-expected ratios > 1.0).

2.9. Assessing hypothetical past and future declines and classifying strongholds

Percentage changes in area with moderate-to-high expected occurrence (i.e., moderate, high, or very high expectation of occurrence) and stronghold area were measured between 2000 and 2020, as well as between 2020 and three future threat scenarios. Current strongholds were then classified by overall threat level, primary threat, and recent camera-trap survey status. For each future threat scenario, we classified current strongholds into one of five threat categories based on predicted declines in area. Strongholds were classified as either very high threat (>30% decline in area qualifying as a stronghold), high threat (10–30% decline), moderate threat (5–10% decline), low threat (<5% decline), or lost (i.e., it no longer qualifies as a stronghold). A stronghold's overall threat level was equivalent to its business-as-usual threat category, while its primary threat (i.e., hunting, forest loss, or both) depended on which individual future threat scenario (high forest loss only or high hunting only) predicted the highest threat category. Strongholds were classified by survey status as either: (1) surveyed and confirmed, (2) surveyed and unconfirmed, or (3) unsurveyed and unconfirmed, based on the results of our literature review (see Section 2.2). Camera-trap surveys that possessed a total survey effort < 500 trap-nights and did not detect golden cats were not included (following Rostro-García et al., 2016). To supplement our classification scheme, we also measured the percentage of each stronghold overlapping a protected area listed by the World Database on Protected

Areas (UNEP-WCMC and IUCN, 2020).

3. Results

3.1. Expectation of occurrence, habitat strongholds, and projected declines

Our top model predicting golden cat occurrence included three variables: mean hunting-induced extirpation risk within a 16 km radius ($\beta = -0.61$ SE 0.09), percentage of the landscape that was closed-canopy (>70% canopy cover) forest within an 8 km radius (0.52 SE 0.14), and mean annual precipitation within an 8 km radius (0.23 SE 0.09). Evaluating our 2020 continuous prediction map with our training data yielded a continuous Boyce index of 0.94, while evaluating the same map with an external dataset (Penjor et al., 2021) yielded a continuous Boyce index of 0.88. Evaluating our 2000 continuous prediction map with an external dataset (records from 1995 to 2005) yielded a continuous Boyce index of 0.84. All three continuous Boyce indices suggest our prediction maps possess at least good predictive accuracy, since the index derived from our training data is likely to be an overestimate.

Across the golden cat's mainland range (Fig. 2) we predicted habitat with moderate-to-high expectation of occurrence to be 518,924 km² in 2020 (Table 1; Fig. 3a), of which 489,719 km² was classified as a habitat stronghold (contiguous areas with moderate-to-high expectation of occurrence $\geq 1,000$ km²; Table 1; Fig. 3b). This marks a 68% decline in area since 2000 for both habitats with moderate-to-high expectation of occurrence (from 1,629,389 km²) and habitat strongholds (from 1,551,338 km²). These predicted declines were primarily driven by changes in hunting-induced extirpation risk (61% decline in moderate-to-high expectation of occurrence when using hunting-induced extirpation risk in 2000 and forest cover in 2019) and not changes in forest cover (15% decline in moderate-to-high expectation of occurrence when using hunting-induced extirpation risk in 2020 and forest cover in 2000). Predicted declines in area for both habitats with moderate-to-high expectation of occurrence and habitat strongholds were greatest in China, Vietnam, Laos, Cambodia, and Myanmar (Table 1). We identified 40 habitat strongholds remaining in 2020 (Table 2). Over half (56%) of the total area classified as a stronghold occurs within just two countries (Myanmar and India) and 83% occurred within trans-

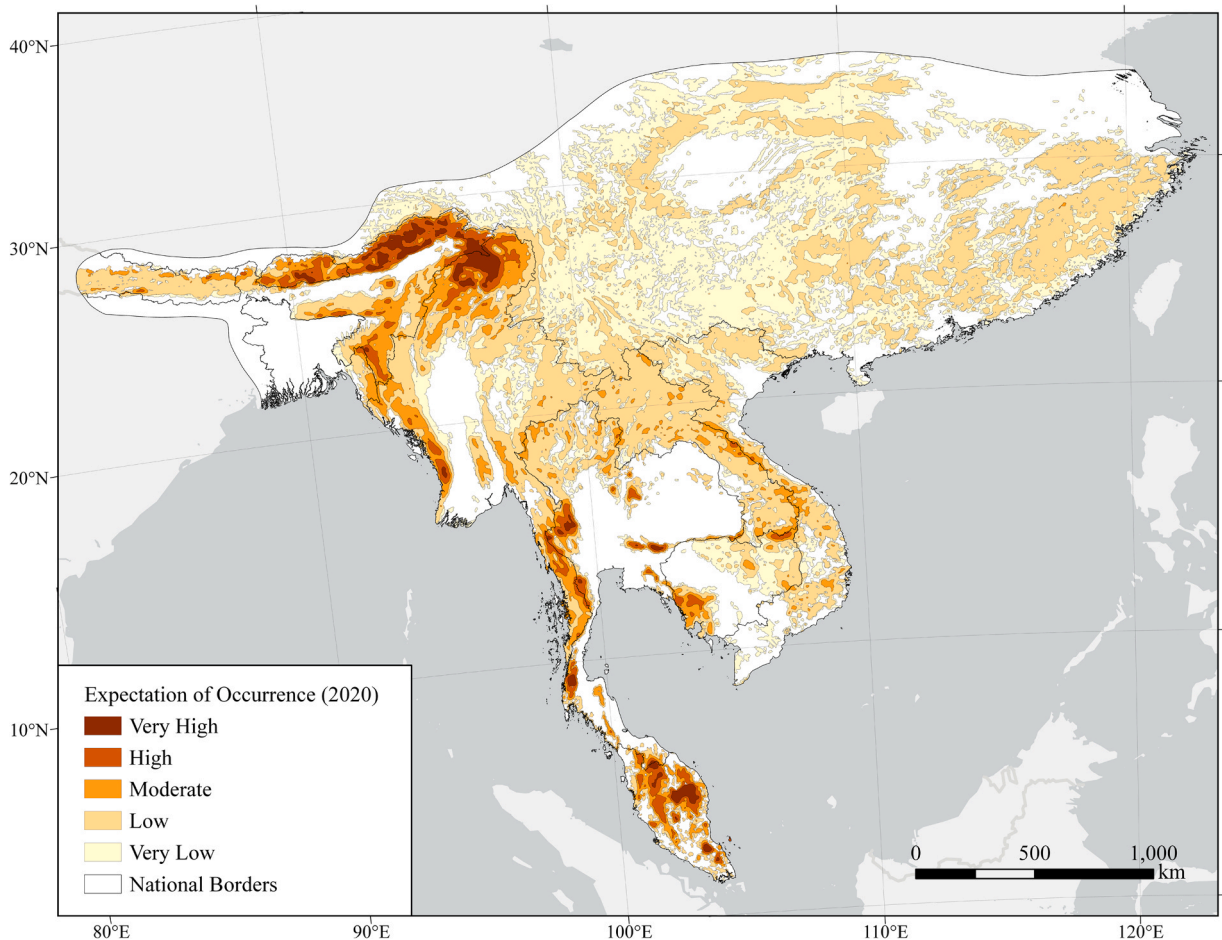


Fig. 2. Expectation of Asian golden cat (*Catopuma temminckii*) occurrence across mainland Southeast Asia in 2020; based on a multi-scale analysis of recent (2010–2020) occurrence records.

Table 1

Area (km²) per range country qualifying as either (a) a habitat stronghold (area with moderate-to-high expectation of occurrence ≥ 1,000 km²) or (b) an area with moderate-to-high expectation of occurrence for Asian golden cat (*Catopuma temminckii*), predicted for the years 2000, 2020, and three future scenarios (2020–2040).

(a) Habitat Strongholds			2020–2040(Hunting and Forest Loss)	2020–2040(Hunting Only)	2020–2040(Forest Loss Only)	Most Pressing Threat (National Level)
Country	2000	2020				
Bangladesh	8,489	6,685	4,757	6,683	4,764	Forest Loss
Bhutan	28,800	29,783	29,582	29,769	29,595	Forest Loss
Cambodia	60,673	19,910	13,305	14,346	15,930	Both
China	475,836	617	365	415	552	Hunting
India	158,905	124,918	119,451	124,293	120,058	Forest Loss
Laos	166,025	19,186	9,714	10,595	18,239	Hunting
Malaysia	77,545	56,503	50,228	56,502	50,228	Forest Loss
Myanmar	364,693	162,038	113,132	120,026	148,191	Hunting
Nepal	7,246	5,864	4,641	5,853	4,653	Forest Loss
Singapore	0	0	0	0	0	–
Thailand	93,377	52,551	39,953	51,954	40,263	Forest Loss
Vietnam	109,749	11,656	6,576	7,237	10,978	Hunting
Total	1551,338	489,711	391,704	427,673	443,451	Hunting

(b) Areas with moderate-to-high expectation of occurrence						
Country	2000	2020	2020–2040(Hunting and Forest Loss)	2020–2040(Hunting Only)	2020–2040(Forest Loss Only)	Most Pressing Threat (National Level)
Bangladesh	8,823	6,741	4,757	6,738	4,764	Forest Loss
Bhutan	28,800	29,785	29,582	29,772	29,595	Forest Loss
Cambodia	63,028	21,281	15,069	16,270	18,191	Both
China	528,393	1,165	466	516	1,069	Hunting
India	159,072	127,027	121,661	126,340	122,365	Forest Loss
Laos	167,012	26,411	14,660	15,706	24,302	Hunting
Malaysia	82,973	57,240	53,290	57,239	53,290	Forest Loss
Myanmar	369,367	167,937	118,374	126,461	153,225	Hunting
Nepal	8,517	8,568	7,750	8,539	7,777	Forest Loss
Singapore	1	0	0	0	0	–
Thailand	100,599	58,285	49,120	57,636	49,572	Forest Loss
Vietnam	112,804	14,484	9,500	10,372	13,146	Hunting
Total	1,629,389	518,924	424,229	455,589	477,296	Hunting

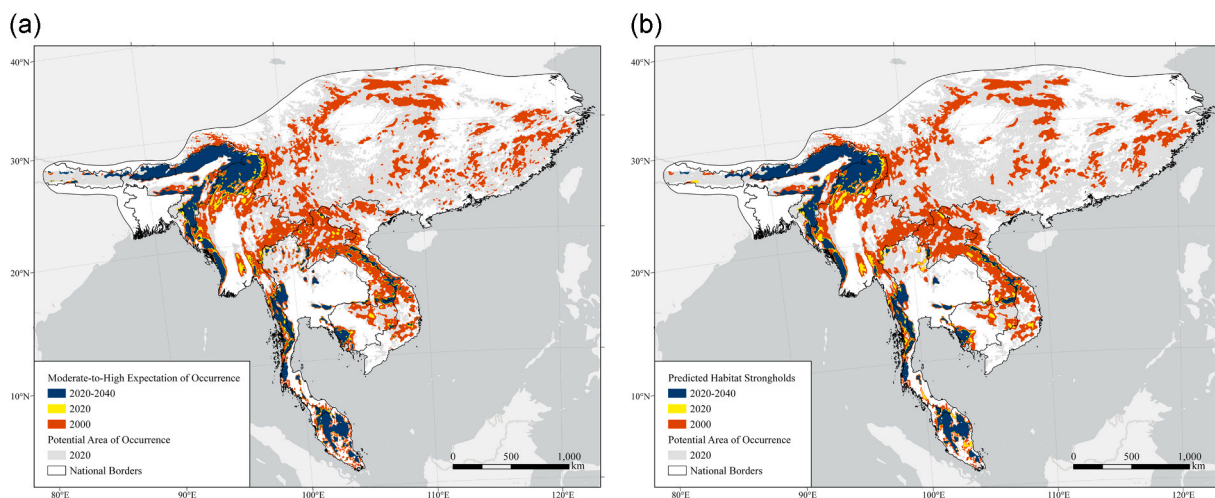


Fig. 3. Areas with (a) moderate-to-high expectation of Asian golden cat (*Catopuma temminckii*) occurrence in 2000, 2020, and the near future (2020–2040; combined hunting and forest loss scenario), along with areas (b) meeting the criteria of a habitat stronghold (contiguous areas of moderate-to-high expectation of occurrence ≥ 1,000 km²) for the same time periods.

boundary strongholds.

Current areas with moderate-to-high expectation of occurrence and habitat strongholds were predicted to decline by 18% and 20%, respectively, over the next 20 years based on a business-as-usual scenario (Tables 1, 2). Based on the same scenario, 17.5% of remaining strongholds were considered low threat, 5% were moderate threat, 25% were high threat, 10% were very high threat, and

Table 2

Summary of remaining (2020) Asian golden cat (*Catopuma temminckii*) habitat strongholds (i.e., areas with moderate-to-high expectation of occurrence $\geq 1000 \text{ km}^2$), including overlap with World Database on Protected Areas-listed protected areas, recent camera-trap survey status (2010–2020), expected declines in stronghold size based on three future scenarios (2020–2040), and primary threat.

Threat Category	Stronghold	Area (km ²) in 2020	Overlap with Protected Areas	Areas Surveyed	Areas with Detections	Area (km ²) in 2020–2040 (Business-as-usual)	Area (km ²) in 2020–2040 (Hunting Only)	Area (km ²) in 2020–2040 (Forest Loss Only)	Primary Threat
Low	9	6,785	73%	1	1	6,675	6,797	6,680	Forest Loss
	11	5,661	27%	2	2	5,619	5,648	5,633	Both
	13	5,127	88%	1	0	5,116	5,127	5,116	Forest Loss
	15	4,655	49%	2	1	4,521	4,655	4,521	Forest Loss
	19	2,500	95%	1	1	2,394	2,500	2,394	Forest Loss
	22	2,144	0%	1	1	2,070	2,144	2,070	Forest Loss
	36	1,247	0%	1	0	1,231	1,247	1,231	Forest Loss
Moderate	3	50,921	13%	9	6	46,576	50,924	46,576	Forest Loss
High	14	4,818	0%	5	3	4,417	4,818	4,417	Forest Loss
	1	193,535	19%	19	18	173,533	177,273	187,487	Hunting Forest
	2	51,834	2%	4	3	42,790	49,123	45,231	Forest Loss
	4	45,672	45%	10	10	37,721	40,112	42,651	Hunting Forest
	5	24,260	7%	2	2	18,216	18,450	23,846	Hunting Forest
	6	14,861	51%	9	1	10,560	11,830	14,134	Hunting Forest
	7	14,024	72%	4	3	10,334	11,317	11,641	Both
	18	2,916	72%	0	0	2,173	2,485	2,554	Both
Very High	24	1,667	77%	0	0	1,458	1,667	1,458	Forest Loss
	28	1,507	40%	1	0	1,352	1,507	1,352	Forest Loss
	29	1,483	96%	1	0	1,193	1,483	1,193	Forest Loss
	8	12,284	60%	7	0	8,282	8,525	11,826	Hunting Forest
	10	5,975	0%	0	0	2,616	4,472	4,546	Both
	12	5,405	2%	2	2	1,753	1,784	4,601	Hunting Forest
	20	2,468	64%	0	0	1,117	2,330	1,145	Forest Loss
Lost	16	3,174	30%	1	1	< 1,000	< 1,000	2,544	Hunting Forest
	17	3,000	43%	0	0	< 1,000	1,706	< 1,000	Both
	21	2,465	0%	0	0	< 1,000	2,465	< 1,000	Forest Loss
	23	1,887	0%	0	0	< 1,000	< 1,000	1,832	Hunting Forest
	25	1,595	65%	0	0	< 1,000	< 1,000	1,545	Hunting Forest
	26	1,548	79%	0	0	< 1,000	1,548	< 1,000	Forest Loss
	27	1,546	74%	0	0	< 1,000	< 1,000	1,380	Hunting Forest
	30	1,431	95%	0	0	< 1,000	< 1,000	1,313	Hunting Forest
	31	1,418	0%	0	0	< 1,000	< 1,000	< 1,000	Both
	32	1,397	93%	1	1	< 1,000	< 1,000	1,370	Hunting Forest
	33	1,375	0%	1	0	< 1,000	< 1,000	< 1,000	Both
	34	1,336	77%	0	0	< 1,000	1,295	< 1,000	Forest Loss
	35	1,324	86%	1	0	< 1,000	< 1,000	1,195	Hunting Forest
37	1,229	94%	0	0	< 1,000	1,229	< 1,000	Forest Loss	
38	1,181	53%	2	0	< 1,000	1,181	< 1,000	Forest Loss	
39	1,042	60%	0	0	< 1,000	1,040	< 1,000	Forest Loss	
40	1,014	83%	0	0	< 1,000	1,014	< 1,000	Forest Loss	

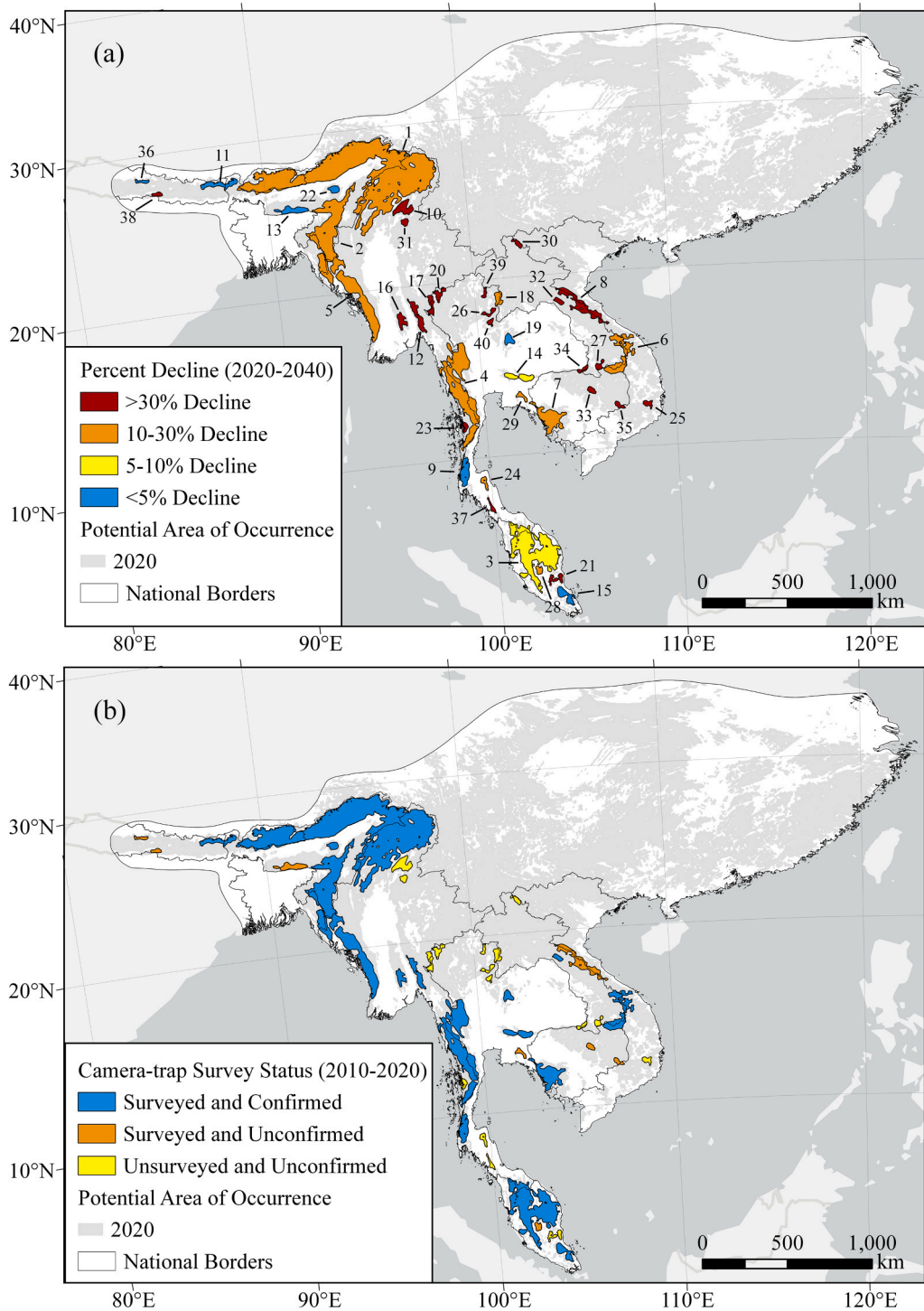


Fig. 4. (a) Asian golden cat (*Catopuma temminckii*) habitat strongholds (2020) classified by percentage decline in area between 2020 and a near future scenario (2020–2040) that includes both hunting and forest loss. (b) Habitat strongholds classified by recent camera-trap survey status (2010–2020). For percentage decline in stronghold area using hunting or forest loss only future scenarios, please refer to [Appendix D](#).

42.5% were lost (i.e., no longer qualifying as strongholds; Table 2; Fig. 4a). Primary threat varied by stronghold (Table 2; Appendix D). Of the remaining strongholds, 50% were primarily threatened by forest loss, 32.5% by hunting, and 17.5% by both (i.e., threat from hunting and forest loss were similarly high).

3.2. Review of recent camera-trap surveys in remaining strongholds

We reviewed the findings from 145 camera-trap surveys between 2010 and 2020 (Appendix E2, E3). Golden cats were detected in 66 surveys. Of the 40 remaining strongholds, 24 had at least one recent camera-trap survey that we could document (Fig. 4b). The presence of golden cats was confirmed from at least one survey in 16 of those 24 strongholds. We found approximately two-thirds (64%) of all documented surveys came from five countries: China (17%), India (13%), Vietnam (13%), Thailand (11%), and Cambodia (10%); 63% of surveys with no detections came from three countries: China (26%), Vietnam (24%), and Cambodia (14%); and 68% of surveys with detections came from four countries: India (22%), Thailand (18%), Myanmar (17%), and Malaysia (11%; Appendix E2). Records suggest widespread occurrence in Bhutan, northeast India, Malaysia, Myanmar, and Thailand; restricted occurrence in Cambodia and Laos; very restricted occurrence in Bangladesh, Nepal, and China; and complete extirpation from Vietnam (Appendix E3). Population density estimates or trends (i.e., increasing, stable, or decreasing) were not known from any survey.

4. Discussion

By delineating where golden cats could be (i.e., areas of moderate-to-high expected occurrence and habitat strongholds), where their threats are predicted to be greatest (i.e., where a business-as-usual near-future scenario predicted the greatest declines in expected occurrence), and where we know the species still occurs (through a literature review), our study not only provides crucial information that can assist with the prioritization of golden cat conservation efforts but also demonstrates an accessible workflow that can be applied to other understudied species. Importantly, this workflow is not limited to a particular set of methodologies, but rather can be tailored to fit available data or the lack thereof. In our study, for example, we were limited to using presence-only data points to model the expected occurrence of golden cats across mainland Tropical Asia. Thus, we used a presence-only species distribution model. However, under different circumstances, we could have used another method to delineate potential occurrence, depending on the quality and quantity of data available, including a presence-absence species distribution model that incorporates imperfect detection (e.g., Zielinski et al., 2015) or even a Bayesian Belief Network (e.g., Tantipisanuh et al., 2014; MacPherson et al., 2018; Phan et al., 2019). Likewise, projecting future occurrence may not always be possible or desirable given the inherent uncertainties involved. In such cases, qualifying threats in some other manner could be just as appropriate, if not more so. Regardless of the method used, it is important to recognize the intention of the workflow presented here is not to perfectly predict species habitat preferences, occurrence probability, or threats, as such an outcome is both unlikely, given the inherent paucity of data available for data-limited species, and unnecessary, as evidenced by past studies investigating the ability for data-limited presence-only species distribution models to guide conservation efforts (Fois et al., 2018). Rather, the objective is to use available data in a straightforward manner to strategically guide future conservation efforts. And because this workflow is not limited to any given methodology, stakeholders are free to repeat the process with new techniques as more, and hopefully, better data become available.

In the following text we provide a top-level overview of our findings, their implications for golden cat conservation efforts in Tropical Asia, and give a few examples demonstrating how our results can be synthesized into actionable conservation assessments at the stronghold and stronghold-complex level. However, we refrain from providing detailed assessments of all 40 habitat strongholds identified in this study as they overlap considerably with previous assessments of clouded leopard habitat strongholds identified and discussed in detail by Petersen et al. (2020). Therefore, we refer the reader to the discussion by Petersen et al. (2020) for detailed assessments that correspond to most strongholds identified in the current golden cat study but not discussed below.

Based on our model results, we predicted the area of moderate-to-high expected occurrence declined by 68% between 2000 and 2020, with a further 18% decline predicted based on the results of a near-future (2020–2040) business-as-usual management scenario (Table 1). Notably, a 68% decline in area of moderate-to-high expected occurrence during the previous 20 years, a period equivalent to three golden cat generations, would suggest the species is more threatened than previously believed and could qualify golden cats for up-listing from Near Threatened to Endangered under IUCN Red List criterion A2c. However, we acknowledge there are limitations to interpreting these results in this manner. In particular, our past and near-future hunting-induced extirpation risk covariates might not reflect historical or near-future hunting risks realistically, despite being based on a combination of spatially-explicit covariates and expert opinion. In addition, our study was limited to mainland Tropical Asia and our findings may not be representative of the species' status elsewhere (i.e., Sumatra). Nevertheless, these predicted declines in areas of moderate-to-high expected occurrence are still worth considering for several reasons. First, they suggest golden cats have undergone, and will probably continue to undergo, substantial population declines across mainland Tropical Asia. Second, we note the primary reason for such a dramatic decline in area of moderate-to-high expected occurrence between 2000 and 2020 was not habitat loss, as we found only a 15% decline range-wide could be attributed to changes in forest cover alone, but rather was the result of a cumulatively increasing hunting-induced extirpation risk across the region (Appendix C1, C3, C6, C7). This finding appears to be consistent with the results of our literature review (Appendix E3). Specifically, our review suggests golden cats may already be extirpated from previously occupied areas across their range despite the continued presence of structurally suitable habitat (e.g., Coudrat et al., 2014; Coudrat, 2019). This is important, as it suggests assessments of conservation status based solely on past declines in habitat (e.g., forest cover) may underestimate actual population declines, particularly in mainland Tropical Asia where hunting is a pervasive threat (Harrison et al., 2016; Gray et al., 2018). Third, our results show declines in expected occurrence have not been, and will probably continue to not be, evenly distributed

throughout mainland Tropical Asia (Table 1). This finding is congruent with the results of our literature review and previous investigations (e.g., Willcox et al., 2014; McCarthy et al., 2015). Ultimately, more data will be needed to say anything for certain concerning the golden cat's true population status and extent of occurrence. Targeted camera-trap surveys in the 16 previously unsurveyed strongholds identified in this study would improve our understanding of the true extent of these apparent declines and should be prioritized accordingly.

Since data on golden cat population status and trends are unavailable, we identified habitat strongholds across mainland Tropical Asia and classified them based on threat level, primary threat, and recent camera-trap survey status, to aid with re-assessment and prioritization efforts. Of the 40 remaining strongholds identified, 78% were classified as either high threat, very high threat, or lost under a business-as-usual near-future scenario; casting doubt on the species' long-term survival in these areas. In addition, our literature review found only 52% of strongholds classified as either high threat, very high threat, or lost, had been surveyed at least once with camera-traps recently, compared to 100% of strongholds classified as either low or moderate threat; highlighting an important limitation for any global assessment of golden cat conservation status, including this study. Although this finding is not unexpected, as research efforts in the tropics are generally biased towards areas with large charismatic species (e.g., tigers) and areas with better protection (which also tend to be where large charismatic species occur; Marshall et al., 2016), it is nevertheless important to recognize. Specifically, failure to acknowledge this bias in survey locations may lead to overly optimistic assessments of conservation status in the future, not only for golden cats but also for other threatened mammals. Importantly, we found both primary threat (e.g., hunting, forest loss) and survey status varied by stronghold. This finding not only highlights the need for stakeholders to tailor their management strategies to local circumstances but actually provides stakeholders with information necessary to facilitate such efforts in a meaningful way. For example, in the Greater Annamite Ecoregion, along the borders between Cambodia, Laos, and Vietnam, we identified six strongholds (6, 8, 25, 27, 32, 35; Fig. 5a), all of which can be considered seriously threatened (i.e., high threat, very high threat, or lost based on the business-as-usual scenario) and primarily threatened by hunting. Due to these threats, only two of the six strongholds (stronghold 6 in the central Annamites and stronghold 8 in the northern Annamites) were predicted to remain as habitat strongholds under our near-future business-as-usual scenario, indicating an urgent need for bold interventions across

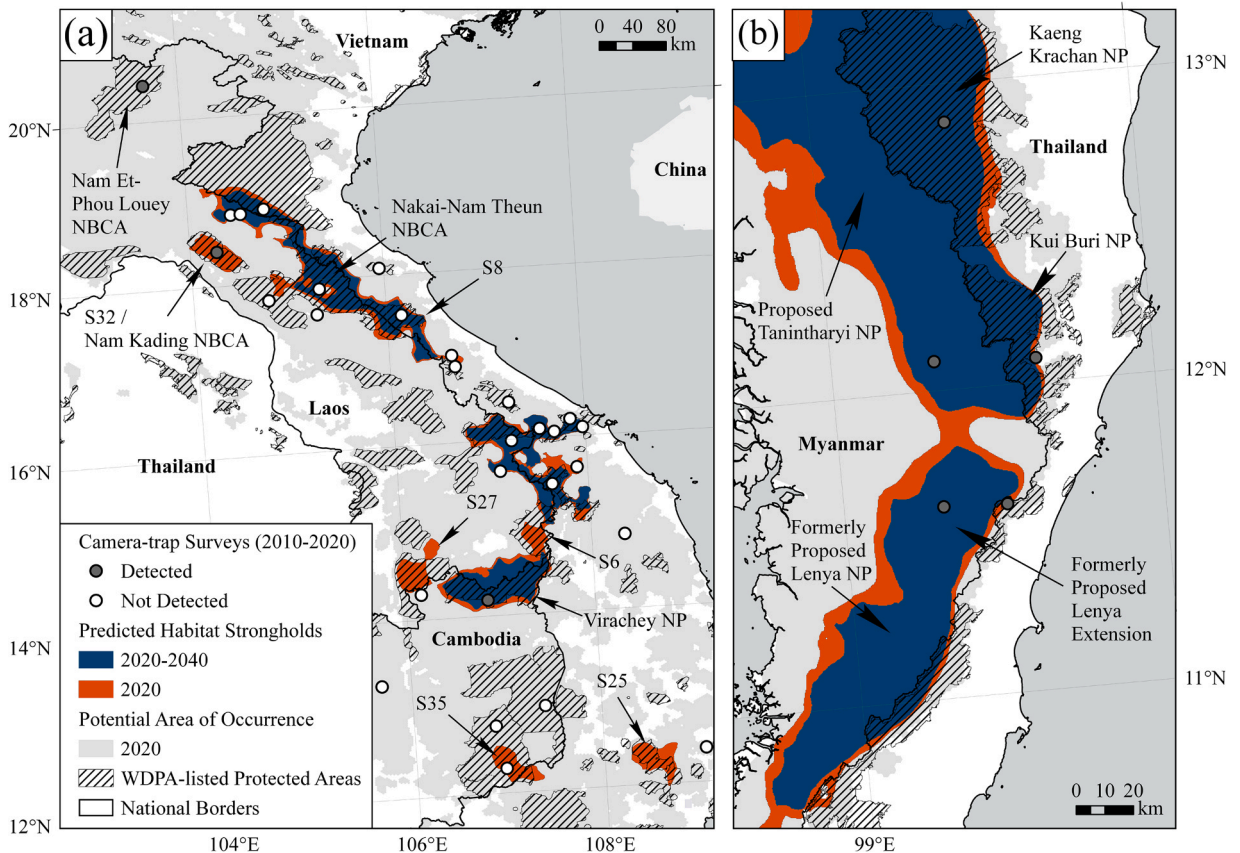


Fig. 5. (a) Asian golden cat (*Catopuma temminckii*) predicted habitat strongholds within the Greater Annamite Ecoregion, showing location of recent camera-trap surveys and protected areas listed by the World Database on Protected Areas (WDPA); including Nam Et-Phou Louey National Biodiversity Conservation Area (NBCA) and Nakai Nam Theun NBCA, Nam Kading NBCA, and Virachey National Park (NP). (b) Predicted habitat strongholds in southern Myanmar, showing location of proposed Tanintharyi NP, and formerly proposed (now dropped) Lenya NP and Lenya NP Extension.

the landscape. Importantly, our literature review found differences in survey status among these strongholds which should be factored into a stakeholder's decision-making process. First, golden cats appear to have been extirpated from all of stronghold 8 (i.e., the northern Annamites), 35 (i.e., Keo Seima Wildlife Sanctuary), and most of 6 (i.e., central Annamites), based on the lack of recent camera-trap records in those areas and despite fairly extensive survey efforts. As such, management of those areas does not appear to be a high priority for golden cat conservation, outside the desire to preserve habitat in the event of future dispersal or reintroductions. Second, two strongholds (stronghold 25, which overlaps Bidoup Núi Bà National Park in southeastern Vietnam, and stronghold 27, which overlaps the Xe Pian National Bio-Diversity Conservation Area in southern Laos) do not appear to have had any recent camera-trap surveys based on the findings of our literature review, and therefore represent possible targets for future surveys. Third, our literature review found records of golden cats from only two locations in the Annamites between 2010 and 2020, once in 2013 at Nam Kading National Biodiversity Conservation Area (central Laos) within stronghold 32 and repeatedly between 2014 and 2020 in Virachey National Park (northeastern Cambodia) within stronghold 6 (McCann et al., 2020); implying that (1) follow-up surveys are needed for Nam Kading to confirm the species' continuing persistence there and (2) that immediate action needs to be taken to mitigate hunting threats in Virachey to preserve what may be among the last remaining population in the Greater Annamite Ecoregion.

The applications of our findings are not only limited to the aforementioned classification scheme. For example, our comparison of current and near-future expectations of occurrence indicates several strongholds are at risk of fragmentation unless successful countermeasures are taken (Fig. 2b). Notably, we found strongholds 4 (i.e., Dawna-Tenassarim Range along the Thai-Myanmar border), 5 (i.e., Arakan Range in western Myanmar), and 6 (i.e., central Annamites along the Cambodia-Lao-Vietnam borders) were all predicted to fragment under a business-as-usual near-future scenario. Fragmentation of these strongholds is cause for concern not only because it indicates a decline in area of potential occurrence, but because it directly threatens population connectivity, gene-flow, and the recolonization of areas where the species has already been extirpated. For example, Virachey may support one of the last surviving populations of golden cats in the central Annamites, if not the entire Annamite Ecoregion (Fig. 5a). If secured, the site could serve as a potential source population for future dispersal throughout the stronghold and the Greater Annamites. However, our business-as-usual scenario predicts the central Annamite stronghold will become fragmented in the near future, a finding that appears to be supported by observations on the ground (McCann et al., 2020), thus threatening the possibility of such dispersal unless targeted interventions are implemented to mitigate losses in connectivity.

In addition to identifying strongholds at risk of fragmentation, it is also possible to highlight potentially valuable locations for the establishment of new protected areas. In general, we found overlap between WDPA-listed protected areas and strongholds to be low throughout the species' range (26% overlap), highlighting an important limitation of the region's current protected area network and its ability to successfully conserve golden cats. Targeted establishment of protected areas could be a prudent management strategy. For example, in southern Myanmar we found the locations of the currently proposed Taninthayi National Park and formerly proposed (now dropped) Lenya National Park and Lenya National Park extension all fell within stronghold 4 of the Dawna-Tenassarim Range, signaling the global importance of these currently unprotected areas (Fig. 5b). However, under our business-as-usual near-future scenario these areas are predicted to shrink and fragment, threatening the long-term viability of golden cat populations there unless successful interventions can be implemented. The official establishment of these protected areas, or others like them, would thus be an especially significant achievement for golden cat conservation efforts in the region.

4.1. Limitations of the stronghold approach

Throughout this study we primarily focus on the largest remaining areas with moderate-to-high expected occurrence, so-called strongholds. Yet, smaller areas with confirmed records do exist and are scattered across the species' range. Given how little we know about golden cats and their capacity to tolerate human disturbance, these areas too should be given consideration, albeit carefully. Notably, the results of our regression model would suggest golden cats may not require vast intact forested landscapes, with highest expected occurrence predicted for forest patches 200 km² or larger, so long as hunting threats across the landscape are kept low. This finding appears consistent with two recent studies from Sumatra (Weiskopf et al., 2019; Haidir et al., 2020). In this regard, it is possible that with enough protection certain areas not identified here as strongholds could potentially support viable populations. Nam Et-Phou Louey National Biodiversity Conservation Area in northern Laos, which was too small to classify as a stronghold, illustrates this point (Fig. 5a). Previously referred to as the "crown-jewel" of Laos' protected area network, Nam Et-Phou Louey received a disproportionate amount of conservation investment over the past two decades in an attempt to save the country's last remaining tigers (*Panthera tigris*; Johnson et al., 2016). These intensive conservation efforts, although insufficient to save the protected area's tigers, may explain why golden cats continue to persist in Nam Et-Phou Louey (Rasphone et al., 2019), but at the same time have disappeared from other protected areas in Laos (e.g., Nakai-Nam Theun National Biodiversity Conservation Area; Coudrat et al., 2014; Coudrat, 2019). Moreover, since no population density estimates for golden cats are available, it is difficult to determine the minimal area necessary to support a viable population. Therefore, we followed previous investigations involving clouded leopards, a sympatric felid with similar body mass and home range size to golden cats (Grassman et al., 2005), and used 1,000 km² as the minimum area needed for habitat to qualify as a habitat stronghold (e.g., Macdonald et al., 2019). However, we acknowledge that our 1,000 km² strongholds may be too small or too large to serve their intended purpose. Hopefully, as more attention shifts towards golden cat conservation and new data become available, we will be able to reevaluate our stronghold definition. In the interim we consider 1,000 km² to be a relatively conservative estimate.

4.2. Additional considerations and future research opportunities

Golden cats exhibit a high degree of ecological plasticity, occurring across a wide range of environmental conditions (McCarthy et al., 2015). As more data on the species become publicly available, it may become worthwhile for stakeholders to account for this plasticity when modeling golden cat occurrence or habitat suitability by using regional distribution models. Past studies have found regional distribution models to be more accurate than global models when modeling the current distribution of highly adaptable species (Vale et al., 2015). A finer-scale regional distribution model may be especially relevant for the ecologically diverse Eastern Himalayas, which overlap most of stronghold 1, the largest stronghold identified by our study (Fig. 4a). Beyond providing a more refined occurrence map for conservation efforts in the region, such an assessment may also explain why golden cats, despite their ecological plasticity, appear to be absent from western and central Nepal, and south of the Indo-Gangetic Plain (McCarthy et al., 2015). For example, our model identified two possible strongholds for the species in central Nepal (36, 38; Fig. 4a). From our model's perspective, strongholds 36 (overlapping Parsa and Chitwan National Parks) and 38 (overlapping Annapurna Conservation Area) tick all the right boxes. They are relatively low risk, possess sufficiently large areas of closed-canopy forest, and receive enough rainfall annually (Appendix C1, C3, C5). Yet the species does not appear to occur in either area; perhaps because of unique (i.e., site-specific) historical factors not accounted for in our coarse hunting-induced extirpation risk model, insufficient connectivity between these potential strongholds and suitable habitats to the east, or because of differences in forest type not accounted for in our study (e.g., the mono-specific, but closed-canopy, sal-forests *Shorea robusta* in Parsa and Chitwan). An Eastern Himalayan regional distribution model may go a long way to answering these questions, with potential conservation implications not only for golden cats but also other closed-canopy dependent species with similar range edges (e.g., clouded leopard, marbled cat *Pardofelis marmorata*).

Declaration of Competing Interest

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01762](https://doi.org/10.1016/j.gecco.2021.e01762).

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