Short communication

A Multi-scale, Multivariate Habitat Selection Model Demonstrates High Potential for the Reintroduction of the Clouded Leopard (*Neofelis nebulosa*) to Taiwan.

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Abstract

Hunting, habitat loss and fragmentation have driven a rapid decline in the distribution and abundance of the clouded leopard, *Neofelis nebulosa*, across its range, and in several areas the species is now extirpated, including Taiwan. Taiwan, an historical stronghold of the species, is a candidate for expanding its current range by reintroduction, based on increasing prey abundance and high forest coverage. Such future reintroduction efforts, however, are hampered by the lack of an empirical analysis of clouded leopard habitat potential in the island. To address this knowledge gap, this study explores the species' habitat suitability in Taiwan. We employed a multi-scale, multivariate habitat selection model based on clouded leopard presence-absence data from extensive camera trap surveys across its current range, and extrapolated the result to predict suitable habitats in Taiwan. Our results reveal that 40% of Taiwanese territory represents suitable habitats for clouded leopards and of which 90% is under protection. This demonstrates the robust potential of Taiwan's habitat for clouded leopard reintroduction.

Keywords

Conservation strategy, Clouded leopard, *Neofelis nebulosa*, multi-scale habitat selection, reintroduction.

The clouded leopard, *Neofelis nebulosa*, is threatened with extinction throughout its range, primarily because of habitat loss and fragmentation, prey exploitation, and direct poaching (Gray et al., 2021). While some regions appear still to contain viable populations, others have witnessed catastrophic declines, and the species is now likely extirpated from Vietnam, most of China, and large parts of Cambodia and Laos (Petersen et al., 2020). One region that has experienced extirpation of clouded leopards is the island of Taiwan. From 1997 to 2012 an extensive camera trap survey of Taiwan's mountainous interior, thought to be the species' last stronghold on the island, failed to reveal any evidence of this felid, and concluded that it had been extirpated some decades ago, likely due to deforestation and over-exploitation of both the species itself and its prey (Chiang et al., 2015). However, the populations of many of Taiwan's mammals are now recovering (Weng et al., 2023), mainly due to an increase of forest cover across the island (Chiu et al., 2015) and the prohibition of hunting (Sun et al., 2019). Buoyed by these changes, and by an overall positive attitude regarding the return of this species to Taiwan among its citizens (Greenspan et al., 2020), a Taiwanese team led by the Clouded Leopard Association of Taiwan (CLAT) and supported by international experts including Panthera, IUCN Cat Specialist Group and the WildCRU is considering a clouded leopard reintroduction programme. This effort, however, is hampered by the lack of an empirical analysis of clouded leopard habitat potential in the island.

To date, only one attempt has been made to quantify available habitat for the clouded leopard in Taiwan. Chiang et al. (2015) used expert opinion of the species' habitat requirements to identify areas of suitable habitat for clouded leopards, and included all forest cover, excluding high elevation coniferous forest, timber monocultures, and anthropogenic features. However, without empirical data on the species itself, the habitat assessment could be biased. Thus, to precisely examine the suitability of habitat for reintroduction efforts, we applied a scale-optimized habitat selection model, developed using extensive camera trap records across the species' range (Macdonald & Bothwell et al., 2019). This allowed us to predict empirically, and to quantify, the potential habitat capacity for clouded leopards in Taiwan.

This study focuses on the main island of Taiwan (Fig. 1), which historically encompassed the most easterly part of the clouded leopard's range. Taiwan is a relatively large (ca 36,000 km^2), rugged, mountainous island that supports a diverse range of habitats, from lowland tropical forest to alpine grassland. Despite significant development in the lowland and coastal regions, over 60% of the island's extent is classified as forest (Chiu et al., 2015) and large swathes of contiguous forest persist in Taiwan's upland interior.

To predict suitable habitats for the clouded leopard in Taiwan, we extrapolated a published habitat suitability model developed across the species' extant range (Macdonald & Bothwell et al., 2019), hereafter referred to as the 'empirical model'. This model was developed using binary presence-absence data of clouded leopards derived from 2,948 camera stations across 45 study areas in nine countries spanning *N. nebulosa's* full range throughout South and Southeast Asia. The resultant data were analysed using a multiscale optimization approach (sensu McGarigal et al., 2016) with a generalized linear mix model (GLMM) to predict clouded leopard habitat suitability. The final model, which is the average model of 4 models with ΔAICc$\leq$2, included 9 environmental variables: (1) percentage of the closed forest, (2) compound topographic index, (3) mean annual precipitation, (4) percentage of cropland/natural vegetation mosaic, (5) correlation length of protected area, (6) correlation length of grassland/shrubland, (7) standard deviation of slope, (8) mean of slope, and (9) percentage of tree cover (Table 1).

We hypothesised that clouded leopard habitat quality in Taiwan would be related to similar factors that drive the distribution of this species on the mainland. We applied the empirical model to Taiwan's environmental conditions, using a combination of the same environmental factors (Table 1) to map predicted suitable habitats for clouded leopards, based on the species' known habitat preferences in mainland areas. Since there are few existing records of clouded leopard occurrence above 3,000 m above sea level, we conservatively removed areas that exceeded this elevation, as they are likely to be used by this felid infrequently. To assess the appropriateness of using the empirical model to extrapolate beyond its original geographical extent, we visually inspected the multivariate environmental similarity surface (MESS, Elith et al., 2010) developed by Macdonald & Bothwell et al. (2019), which provides an index of similarity between the conditions at sampling locations used for model development and the environmental space in Taiwan.

To provide further insight into the potential clouded leopard reintroduction capacity of Taiwan, we reclassified the continuous habitat suitability surface into three classes, using a range of increasingly stringent thresholds of suitability: unsuitable (<75^{th} percentile), moderately suitable ($\geq 75^{th}$ percentile) and highly suitable ($\geq 90^{th}$ percentile). Last, we compared and overlapped the classified suitable habitat surface with (1) Chaing et al.'s (2015) clouded leopard habitat prediction, which relied on expert opinions, hereafter referred to as the 'expert model' and (2) the Protected Areas Network in Taiwan (UNEP-WCMC, 2024).

Our predictive model suggests that a large (13,853 km^2), contiguous area in Taiwan's hilly and mountainous interior, constituting 37.95% of the island's landmass, is composed of moderately (10,040 km^2) and highly (3,812 km^2) suitable habitat for clouded leopards (Fig. 2a; Table 2). Inspection of Macdonald & Bothwell et al's (2019) MESS analysis indicates that the multivariate environmental space encompassed by the empirical model's training data was highly similar to conditions encountered throughout the areas in Taiwan that are predicted as being suitable habitat, which suggests that extrapolation of this model to Taiwan is viable. Our findings corroborate Chiang et al's (2015) expert model in those areas the model predicted to be suitable habitat are also predicted to be suitable in our model. However, our model predicts a much larger area of moderately to highly suitable habitat than the expert model, which estimated that suitable clouded leopard habitat covered only 8,523 km^2 (Fig. 2b). Intersection analysis reveals that 45.9% of the area predicted as suitable for clouded leopard is under protection, of which 3,418.5 km^2 (89.66%) and 2,940.4 km^2 (29.28%) are highly and moderately suitable habitats, respectively (Fig. 2c).

Our extrapolation of an optimized empirically based habitat model for clouded leopards on the Asian mainland to Taiwan predicted extensive and connected habitat within Taiwan's rugged, mountainous terrain. Additionally, our habitat suitability predictions are largely in agreement with the expert model for the areas of highest suitability but suggest that the suitable habitat may be much more extensive and integrated than previously thought. Our results indicated vastly more suitable habitat than did the expert model, which might result from different perspectives regarding anthropogenic impacts on the species. Chiang et al.'s (2015) study classified several areas as unsuitable based on the proximity to roads and human settlements. However, considering the uncertain influence of road proximity on the species (Kaszta et al. 2020), we conservatively included suitable habitats even if there were neighbouring roads. While hunting pressure is known to affect species' distribution on the mainland (Petersen et al. 2020), hunting pressure on Taiwan is likely to be low given that long-standing and effective hunting prohibition (Sun et al. 2019).

Importantly, our results reveal that 89.66% of the highly suitable habitats for clouded leopards are protected in Taiwan, exceeding the protection rates of most core habitats in Southeast Asia (Macdonald & Bothwell et al. 2019). Even when accounting for all potential habitats (moderately to highly suitable), 45.9% are under protection—still above the Southeast Asian mainland average of 31.46%. Taiwan's substantial habitat protection, coupled with likely low hunting pressure, positions it as an excellent candidate for the clouded leopard reintroduction.

It is not known how well the model from Macdonald et al. (2019), developed across the mainland extent range of the clouded leopard, extrapolates to Taiwan. It is possible that the model may overestimate the extent of suitable habitat due to the fact that it subsumed continental scale variation into a single global model, ignoring potential nonstationarity in local limiting factors and realized habitat niche (e.g., Cushman et al. 2024 a, b, c, d). Nonetheless, statistical extrapolation of a habitat model developed from a very large empirical database is likely the best means currently available to assess habitat potential for clouded leopard in Taiwan. Last, this study is preliminary and limited with respect to, for example, prey distribution and abundance, functional connectivity, and social feasibility, which should be considered while developing more refined plans for this reintroduction effort. Nonetheless, this study represents the first empirically-based attempt to predict habitat suitability for the clouded leopard in Taiwan and will be of value to garner support for, and to help underpin strategies for, the reintroduction of this iconic species.

Author contributions

Study design: YFW, AJH; data analysis YFW, ZK; writing: all authors.

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Conflicts of interest

None.

Ethical standards

This study follows the ethical standards stated in Oryx's guideline.

Data availability

(1) Macdonald & Bothwell et al.'s (2019) camera trapping dataset is available upon request, but (2) Chiang et al.'s (2015) and UNEP-WCMC's (2024) layers could be access via Oryx's and UNEP-WCMC's websites.

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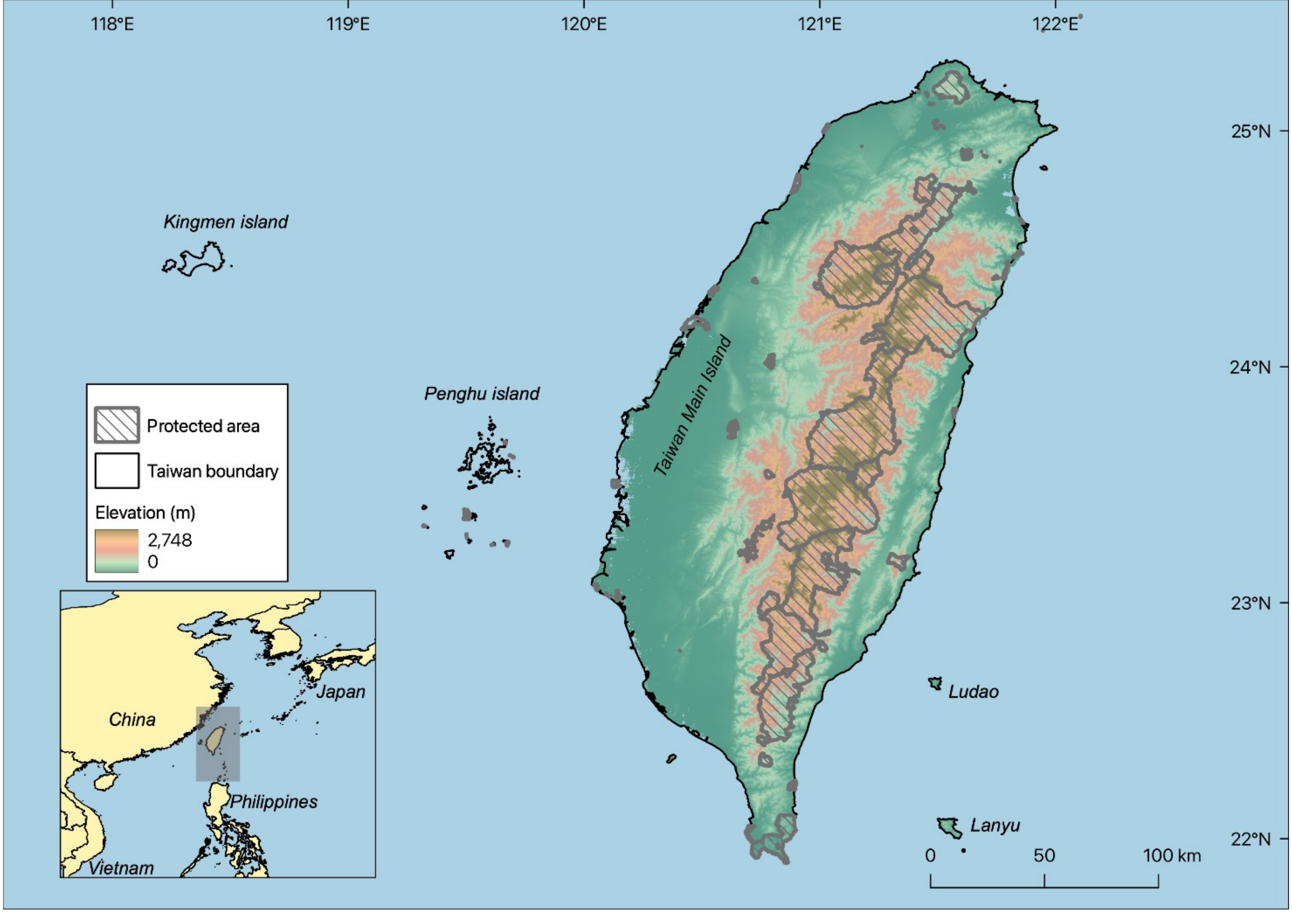
118°E
119°E
120°E
121°E
122°E
25°N
24°N
23°N
22°N
Kingmen island
Penghu island
Taiwan Main Island
Ludao
Lanyu
Protected area
Taiwan boundary
Elevation (m)
2,748
0
China
Japan
Philippines
Vietnam
0
50
100 km

Figure 1. The island of Taiwan, with elevation and the Protected Areas Network shown.

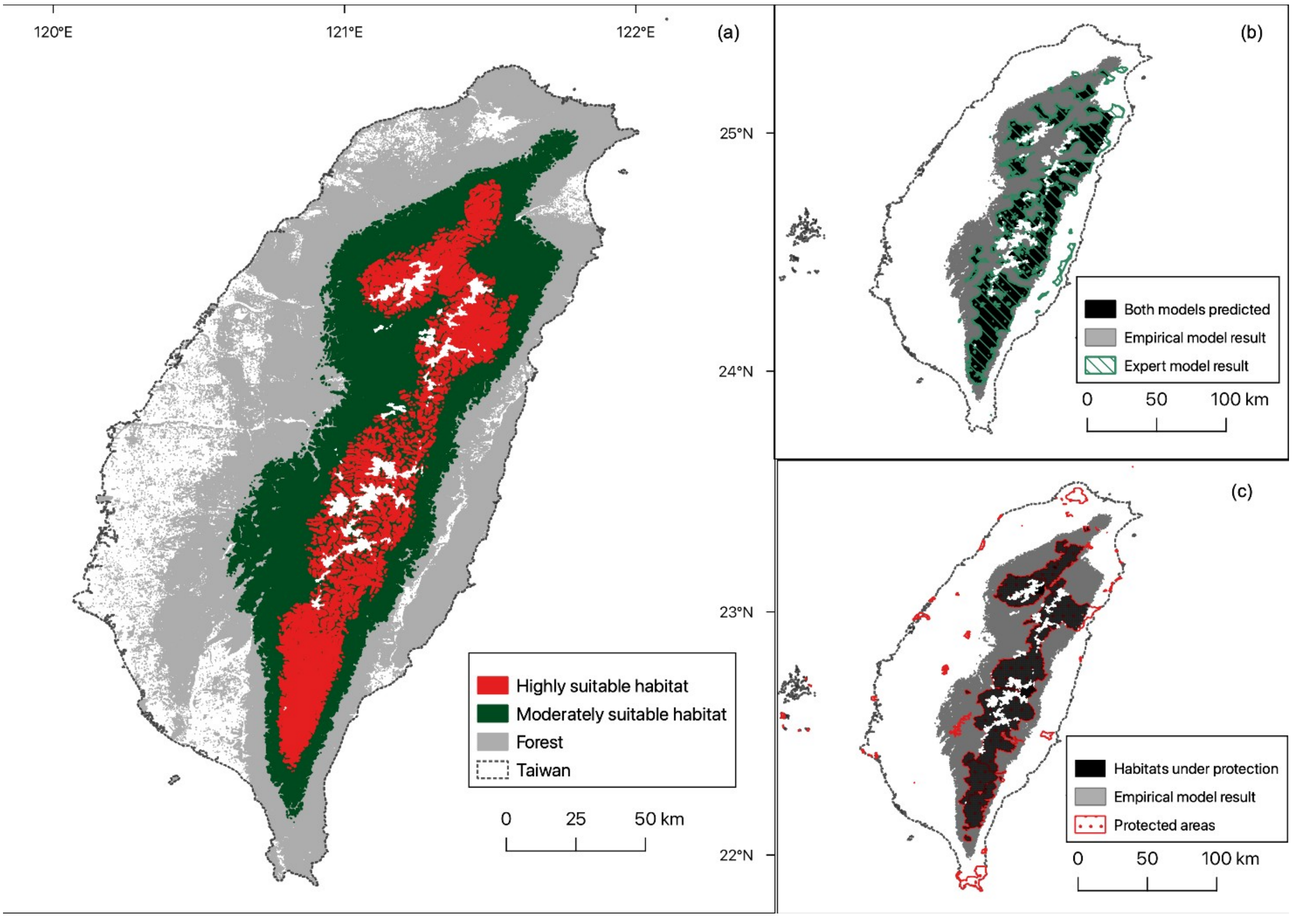

Figure 2. (a) Predicted suitable habitat for *N. nebulosa* in Taiwan; intersection analyses showing overlaps between the Empirical model and (b) the Expert model, and (c) Protected Areas Network in Taiwan.

Table 1. Covariates – camera efforts and other 9 environmental variables, included in Macdonald's top four multi-scale GLMM models with the optimal scale, AIC importance, averaged and adjusted SE β (coefficient), z, and p-value of each covariate.

Fixed effects	**Optimal scale (m)**	**AIC imp.**	**Model averaged β**	**Adjusted SE β**	**z**	**p**
(Intercept)			-1.7532	0.1367	12.829	<0.0001
Camera efforts (# trap days)			0.2244	0.0132	16.966	<0.0001
% Closed forest	16000	1	0.6464	0.1017	6.354	<0.0001
Compound topographic index focal mean	500	1	-0.2569	0.0514	4.999	<0.0001
Mean annual precipitation focal mean	32000	1	0.4000	0.0965	4.146	0.0002
% Mosaic	1000	1	-0.3709	0.0925	4.012	<0.0001
Protected area correlation length	8000	1	0.1937	0.0748	2.591	0.0096
Shrubland/ grassland correlation length	16000	1	0.2722	0.0619	4.398	<0.0001
Slope position SD	500	0.78	0.0702	0.0570	1.232	0.2180
Slope position focal mean	8000	0.17	0.0027	0.0167	0.160	0.8732
% Tree cover	16000	0.17	0.0073	0.0629	0.117	0.9070

Table 2. The geometric result of the empirical model and the overlapped analysis between the empirical model and (b) the expert model, and (c) Protected Areas Network in Taiwan.

		Suitable habitat predicted in this study			Expert model	Taiwan
		Highly	Moderately	Total		
Source		This study	This study	This study	Chiang et al. (2015)	-
Area (km^2)		3,812.67	10,040.87	13,853.54	8,523.00	36,505.00
Area in Protected Areas	Area (km^2)	3,418.48	2,940.36	6,358.84		
	Percentage	89.66%	29.28%	45.9%		
Area in Expert Model	Area (km^2)	2,276.89	3,887.01	6,163.9		
	Percentage	59.72%	38.71%	44.49%		
Area in Taiwan	Percentage	10.44%	27.51%	37.95%		