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 caused a rapid decline in the distribution and abundance of the clouded leopard *Neofelis nebulosa* across its range, and in several areas, including Taiwan, the species is now extirpated. Taiwan, a former stronghold for the species, is a candidate for its reintroduction, based on increasing prey abundance and high forest coverage. Such future reintroduction efforts, however, are hampered by a lack of analysis of potential clouded leopard habitat on the island. To address this, we explore habitat suitability for the species in Taiwan. We used a multi-scale, multivariate habitat selection model based on clouded leopard presence–absence data from extensive camera-trap surveys across its current range to predict suitable habitat in Taiwan. Our findings indicate that 38% of Taiwanese territory is potentially suitable habitat for the clouded leopard, of which 46% is under protection. This demonstrates the high potential of Taiwan's habitat for clouded leopard reintroduction.

Keywords Clouded leopard, conservation strategy, habitat suitability, multi-scale habitat selection, *Neofelis nebulosa*, reintroduction, Taiwan

The clouded leopard *Neofelis nebulosa*, categorized as Vulnerable on the IUCN Red List, is threatened throughout its range, primarily because of habitat loss and fragmentation, prey exploitation and poaching (Gray et al., 2021). While viable populations may remain in some regions, others have undergone catastrophic declines and the species has probably been extirpated from Viet Nam, most of China and large parts of Cambodia and Laos (Petersen et al., 2020). Another region that has experienced extirpation of the clouded leopard is the island of Taiwan. During 1997–2012, an extensive camera-trap survey of Taiwan's mountainous interior, believed to be the species' last stronghold on the island, did not find any evidence of the felid, and it was concluded the species had been extirpated decades earlier, probably as a result of deforestation and overexploitation of both the clouded leopard and its prey (Chiang et al., 2015). However, populations of many of Taiwan's mammals are now recovering (Weng et al., 2023), mainly because of an increase in forest cover across the island (Chiu et al., 2015) and the prohibition of hunting in the 1970s (Sun et al., 2019). Encouraged by this and a positive attitude regarding the return of the species among Taiwanese citizens (Greenspan et al., 2020), a team led by the Clouded Leopard Association of Taiwan and supported by international experts from Panthera, the IUCN Species Survival Commission Cat Specialist Group and The Wildlife Conservation Research Unit is considering a clouded leopard reintroduction programme in Taiwan. However, the programme is hampered by a lack of analysis of potential suitable clouded leopard habitat on the island.

To date, only one attempt has been made to quantify available habitat for the clouded leopard in Taiwan. Chiang et al. (2015) identified areas of suitable habitat for the clouded leopard based on prior knowledge of the species' habitat requirements. However, without empirical data on the species itself, the habitat assessment could be biased. Thus, to examine the availability of suitable habitat for reintroduction, we applied a multi-scale multivariate habitat selection model, developed using extensive camera-trap records from across the species' range (Macdonald et al., 2019). This allowed us to predict and quantify potential habitat for the clouded leopard in Taiwan.

We focused on the main island of Taiwan, which historically encompassed the most easterly part of the clouded leopard's range. At c. 36,000 km^2, Taiwan is a relatively large, rugged and 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 is classified as forest (Chiu et al., 2015) and large swathes of continuous forest persist in the upland interior.

To predict suitable habitat for the clouded leopard in Taiwan, we extrapolated a habitat suitability model developed for the species' extant range (Macdonald et al., 2019), hereinafter referred to as the empirical model. This empirical model was developed using binary presence–absence data of clouded leopards derived from 2,948 camera-trap stations across 45 study sites in nine countries, spanning

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the full range of *N. nebulosa* throughout South and Southeast Asia. Macdonald et al. (2019) analysed these data with a multi-scale optimization approach (sensu McGarigal et al., 2016) with a generalized linear mixed model to predict clouded leopard habitat suitability. The empirical model, which averages four models with ΔAICc ≤ 2 (difference in Akaike information criterion corrected for small sample size, compared to the best performing model), incorporates nine environmental variables: (1) per cent of closed forest (forest cover > 40%), (2) mean compound topographic index (i.e. flow accumulation, with lower values in higher elevation areas), (3) mean annual precipitation, (4) per cent of mosaic land cover (i.e. mixed land cover types), (5) correlation length (i.e. the average distance an individual can travel within habitat patches) of protected area, (6) correlation length of grassland/shrubland, (7) standard deviation of slope, (8) mean of slope, and (9) per cent of tree cover. All covariates are defined in Macdonald et al. (2019).

We hypothesized that clouded leopard habitat quality in Taiwan would be influenced by similar factors to those that drive the species' distribution elsewhere. 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 based on the species' known habitat preferences elsewhere. As there are few records of clouded leopard occurrence above 3,000 m, we removed areas that exceeded this elevation, as they are likely to be used 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 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 for clouded leopard reintroduction in Taiwan, we grouped the continuous habitat suitability surface into three classes, using a range of increasingly stringent thresholds of suitability: unsuitable (< 75th percentile), moderately suitable (≥ 75th percentile) and highly suitable (≥ 90th percentile). Lastly, we compared the suitable habitat with (1) Chaing et al.'s (2015) prediction of clouded leopard habitat, which relied on expert opinions, hereinafter referred to as the expert model, and (2) the protected areas network in Taiwan (UNEP-WCMC, 2024).

Our predictive model suggests that a large, continuous area of 13,854 km² (38% of the island's landmass) in Taiwan's hilly and mountainous interior, is composed of moderately (10,041 km²) and highly (3,813 km²) suitable habitat for the clouded leopard (Fig. 1a; Table 2). Inspection of Macdonald et al.'s (2019) multivariate environmental similarity surface indicates that the multivariate environmental space used for training of the empirical model was similar to the environmental conditions in areas of predicted suitable habitat in Taiwan, suggesting that extrapolation of this model to Taiwan is viable. Our findings corroborate Chiang et al.'s (2015) expert model, with areas they predicted to be suitable habitat also being predicted as suitable by our model. However, our model predicted a much larger area of moderately to highly suitable habitat than the expert model, which estimated suitable clouded leopard habitat to be only 8,523 km² (Fig. 1b). Intersection analysis shows that 46% of the area predicted by our model as suitable for the clouded leopard is under protection, of which 3,419 km² (90%) and 2,940 km² (29%) are highly and moderately suitable habitats, respectively (Fig. 1c).

Our extrapolation of an optimized empirically based habitat model for the clouded leopard on the Asian mainland to the island of Taiwan predicted extensive and connected habitat within Taiwan's rugged, mountainous terrain. Additionally, our habitat suitability predictions largely align with the expert model for the areas of highest suitability

Table 1 Camera-trap days and combination of nine environmental variables included in the empirical model (Macdonald et al., 2019) when used to project the suitable habitat for the clouded leopard *Neofelis nebulosa* in Taiwan, with the optimal scale, Akaike information criterion (AIC) importance, averaged and adjusted standard error *β* (coefficient) for four models, *z*, and P-value of each covariate. (The AIC importance is the importance of a covariate in improving the model when it is included. It is calculated as the sum of the Akaike weights for all models that include the 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-trap days			0.2244	0.0132	16.966	< 0.0001
Per cent closed forest	16,000	1	0.6464	0.1017	6.354	< 0.0001
Mean of compound topographical index	500	1	−0.2569	0.0514	4.999	< 0.0001
Mean annual precipitation	32,000	1	0.4000	0.0965	4.146	0.0002
Per cent mosaic land cover	1,000	1	−0.3709	0.0925	4.012	< 0.0001
Correlation length of protected area	8,000	1	0.1937	0.0748	2.591	0.0096
Correlation length of shrubland/grassland	16,000	1	0.2722	0.0619	4.398	< 0.0001
Slope position (standard deviation)	500	0.78	0.0702	0.0570	1.232	0.2180
Slope position (mean)	8,000	0.17	0.0027	0.0167	0.160	0.8732
Per cent tree cover	16,000	0.17	0.0073	0.0629	0.117	0.9070

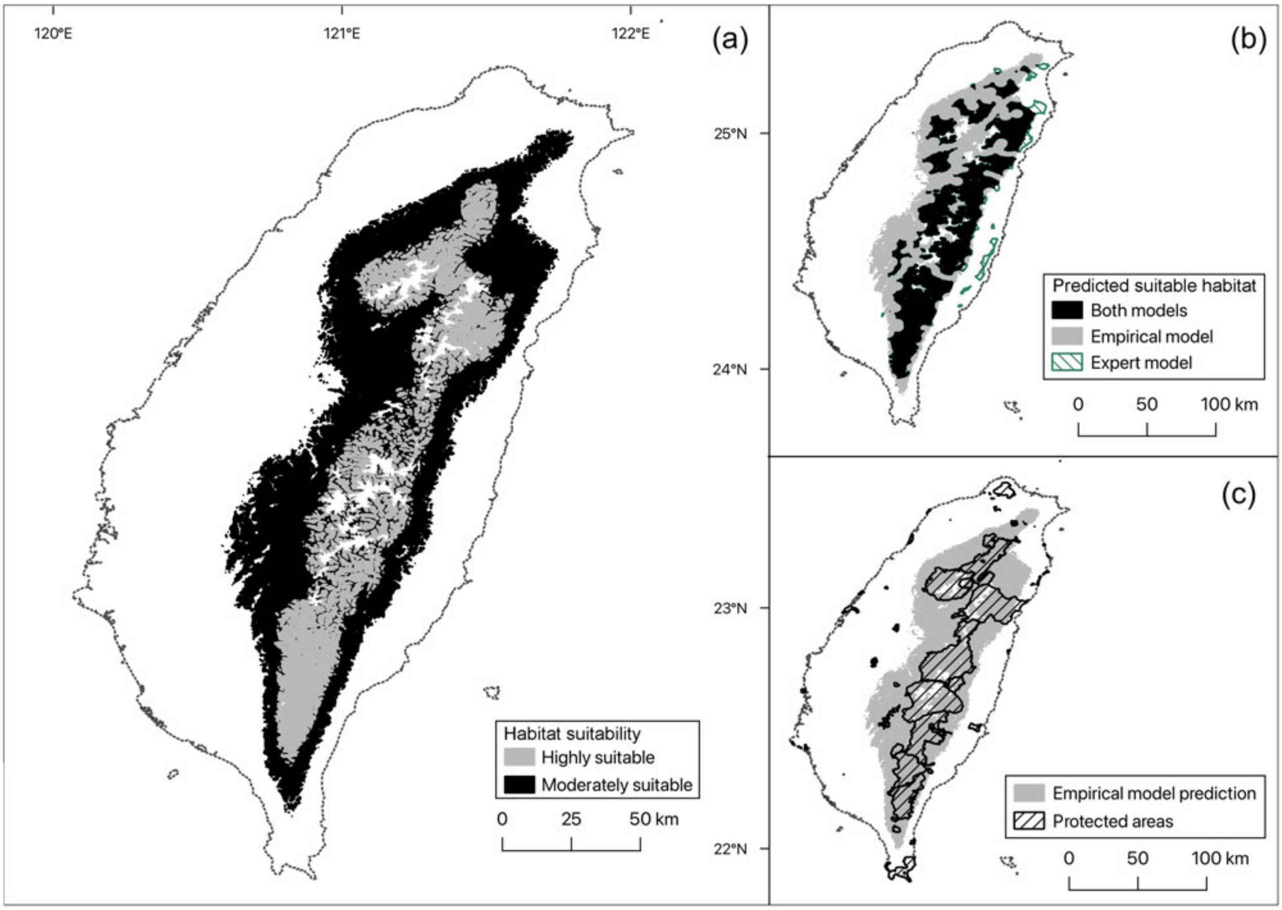

Fig. 1 (a) Predicted suitable habitat for the clouded leopard *Neofelis nebulosa* in Taiwan. (b) Comparison of suitable habitat predicted by applying the empirical model (Macdonald et al., 2019) to Taiwan and by the expert model (Chiang et al., 2015). (c) Protected areas network in Taiwan (UNEP-WCMC, 2024) and suitable habitat predicted by application of the empirical model.

Table 2 Highly and moderately suitable habitat predicted by the empirical model when applied to Taiwan, with the predicted suitable habitat within protected areas in Taiwan, the predicted suitable habitat that overlaps with the expert model (Chaing et al., 2015), and the total predicted suitable habitat as a per cent of the total land area of Taiwan.

Empirical model when applied to Taiwan	Highly suitable	Moderately suitable	Total
Total area of predicted suitable habitat (km^2)	3,812.67	10,040.87	13,853.54
Predicted suitable habitat within protected areas (km^2; UNEP-WCMC, 2024) (% of total)	3,418.48 (90%)	2,940.36 (29%)	6,358.84 (46%)
Predicted suitable habitat overlapping with the expert model (km^2; Chiang et al., 2015) (% of total)	2,276.89 (60%)	3,887.01 (39%)	6,163.9 (45%)
Per cent of total land area of Taiwan	10	28	38

but suggest that the suitable habitat could be more extensive than predicted by the latter. The difference in predicted suitable habitat between models could result from different perspectives regarding anthropogenic impacts on the species. Chiang et al. (2015) 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 included suitable habitats even if they were close to roads. Although hunting pressure is known to affect the species' distribution on the mainland (Petersen et al., 2020), hunting pressure in Taiwan is likely to be low because of the country's long-standing and effective hunting bans (Sun et al., 2019).

Our results show that 90% of the predicted highly suitable clouded leopard habitat in Taiwan is protected, exceeding the protection rates of most core habitats in Southeast

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Asia (Macdonald et al., 2019). When also including moderately suitable habitat, 46% of all suitable habitat is under protection, still above the Southeast Asian mainland average of 32%. Taiwan's substantial habitat protection, coupled with low hunting pressure, suggests it could be suitable for reintroduction of the clouded leopard.

It is possible, however, that extrapolating Macdonald et al.'s (2019) empirical model to Taiwan could overestimate the extent of suitable habitat because it subsumes continental scale variation into a single global model, ignoring potential nonstationarity in local limiting factors and realized habitat niche (i.e. island and continental difference in climate dynamics or sympatric species; e.g. Cushman et al., 2024a,b,c,d). Nonetheless, statistical extrapolation of a habitat model developed from a large empirical database is probably the best method currently available to assess habitat potential for the clouded leopard in Taiwan. Finally, this study is preliminary and limited with respect to prey distribution and abundance, functional connectivity and social feasibility, all of which should be considered in the development of more refined plans for this proposed reintroduction. Our study is the first empirically-based attempt to predict habitat suitability for the clouded leopard in Taiwan and will be of value to develop strategies and garner support for the reintroduction of this iconic species.

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Conflicts of interest None.

Ethical standards This study abided by the *Oryx* guidelines on ethical standards.

Data availability The camera-trapping dataset used by Macdonald et al. (2019) is available upon request from D.W. Macdonald. The model used in Chiang et al. (2015) is available open access in *Oryx*. UNEP-WCMC (2024) data can be accessed via the UNEP-WCMC's website.

References

Chiang, P.J., Pei, K.J.C., Vaughan, M.R., Li, C.F., Chen, M.T., Liu, J.N. et al. (2015) Is the clouded leopard *Neofelis nebulosa* extinct in Taiwan, and could it be reintroduced? An assessment of prey and habitat. *Oryx*, 49, 261–269.

Chiu, L.W., Huang, C.S., Wu, J.C. & Hsieh, S.T. (2015) The fourth national forestry resource assessment report. *Taiwan Forestry Journal*, 41, 3–13. [In Mandarin].

Cushman, S.A., Kilshaw, K., Campbell, R.D., Kaszta, Z., Gaywood, M. & Macdonald, D.W. (2024a) Comparing the performance of global, geographically weighted and ecologically weighted species distribution models for Scottish wildcats using GLM and random forest predictive modeling. *Ecological Modelling*, 492, 110691.

Cushman, S.A., Kilshaw, K., Kaszta, Z., Campbell, R.D., Gaywood, M. & Macdonald, D.W. (2024b) Variable importance and scale of influence across individual Scottish wildcat hybrid habitat models. *Ecological Modelling*, 491, 110698.

Cushman, S.A., Kilshaw, K., Kaszta, Z., Campbell, R.D., Gaywood, M. & Macdonald, D.W. (2024c) Explaining inter-individual differences in habitat relationships among wildcat hybrids in Scotland. *Ecological Modelling*, 491, 110656.

Cushman, S.A., Kilshaw, K., Kaszta, Z., Campbell, R.D., Gaywood, M. & Macdonald, D.W. (2024d) Exploring nonstationary limiting factors in species habitat relationships. *Ecological Modelling*, 490, 110663.

Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330–342.

Gray, T., Borah, J., Coudrat, C.N.Z., Ghimirey, Y., Giordano, A., Greenspan, E. et al. (2021) *Neofelis nebulosa*. In *The IUCN Red List of Threatened Species* 2021. dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T14519A198843258.en.

Greenspan, E., Giordano, A.J., Nielsen, C.K., Sun, N.C.M. & Pei, K.J.C. (2020) Taiwanese attitudes toward the clouded leopard (*Neofelis nebulosa*) and its potential reintroduction. *Human Dimensions of Wildlife*, 25, 301–323.

Kaszta, Ż, Cushman, S.A., Htun, S., Naing, H., Burnham, D. & Macdonald, D.W. (2020) Simulating the impact of belt and road initiative and other major developments in Myanmar on an ambassador felid, the clouded leopard, *Neofelis nebulosa*. *Landscape Ecology*, 35, 727–746.

Macdonald, D.W., Bothwell, H.M., Kaszta, Ż, Ash, E., Bolongon, G., Burnham, D. et al. (2019) Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis nebulosa*). *Diversity and Distributions*, 25, 1639–1654.

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C. & Cushman, S.A. (2016) Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology*, 31, 1161–1175.

Petersen, W.J., Steinmetz, R., Sribuarod, K. & Ngoprasert, D. (2020) Density and movements of mainland clouded leopards (*Neofelis nebulosa*) under conditions of high and low poaching pressure. *Global Ecology and Conservation*, 23, e01117.

Sun, N.C.M., Arora, B., Lin, J.S., Lin, W.C., Chi, M.J., Chen, C.C. et al. (2019) Mortality and morbidity in wild Taiwanese pangolin (*Manis pentadactyla pentadactyla*). *PLOS One*, 14, e0198230.

UNEP-WCMC (2024) *Protected Area Profile for Taiwan, Province of China from the World Database on Protected Areas*. protectedplanet.net/en [accessed 1 February 2024].

Weng, G.J., Liu, J.N., & Tuanmu, M.N. (2023) Optimization and Data Integration of the Long-term Monitoring System for Wildlife. Term report of Forestry Bureau, Taipei, Taiwan. [In Mandarin]