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# Habitat Suitability Modeling for Endangered Pangolins

**Helena Costa[1], Andreas Ivanov[2], Andreas Klein[3]**

[1] Research Scientist, Department of Computer Science, Advanced Computing University, Paris, France. Email: helena.costa39@yahoo.com| ORCID: 5594-1514-3654-1134
[2] Postdoctoral Researcher, Department of Machine Learning, Baltic AI Research University, Tallinn, Estonia. Email: andreas.ivanov133@yahoo.com | ORCID: 3633-0664-5423-1811
[3] Postdoctoral Researcher, Institute of Intelligent Systems, Nordic Technical University, Stockholm, Sweden. Email: andreas.klein738@yahoo.com | ORCID: 5359-8337-2597-7744

**ABSTRACT**

*Pangolins (Order Pholidota; Family Manidae; 8 species) are the world's most heavily trafficked wild mammals, with an estimated one million individuals removed from the wild between 2000 and 2013 for the traditional medicine and bushmeat trade -- driving all eight species to threatened status on the IUCN Red List. Effective conservation planning for pangolins is constrained by severe data deficiency: most species have limited confirmed locality data, no comprehensive population estimates, and minimal quantitative habitat characterisation -- limiting the species distribution models and connectivity analyses needed to identify priority conservation areas and movement corridors. This study presents the most comprehensive ensemble habitat suitability modelling analysis for pangolins yet conducted, integrating 8,470 quality-filtered occurrence records for all 8 species with 14 environmental predictor variables and novel camera trap survey data from 247 sites across sub-Saharan Africa and South/Southeast Asia to produce validated models and identify priority conservation landscapes. Current suitable habitat averaged 184,700 +- 84,700 km2 per species but 74.8% of suitable habitat falls outside designated protected areas. Under RCP 8.5 (2070), mean habitat loss was -34.7% +- 14.7%. Poaching pressure index (based on seizure records and human access) was the single strongest predictor of pangolin occurrence (partial R2 = 0.64) -- outweighing all environmental variables -- confirming that wildlife crime pressure is now the primary driver of pangolin distribution. Connectivity modelling identified 84 priority corridors linking fragmented populations, 64.7% of which cross major road infrastructure.*

**Keywords:** pangolins; Manidae; Manis; Smutsia; habitat suitability; MaxEnt; wildlife trafficking; connectivity corridors

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## 1. Introduction

### 1.1 Pangolins: The World's Most Trafficked Mammal

The pangolins -- eight species of insectivorous, scale-covered mammals in the Order Pholidota -- represent one of the most acute wildlife conservation crises of the 21st century: all eight species are listed as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List, and the order as a whole is estimated to be the most heavily trafficked group of mammals globally. An estimated one million pangolins were removed from the wild between 2000 and 2013 for the traditional Chinese medicine trade (where pangolin scales are used in treatments for a wide range of conditions despite lacking any demonstrated efficacy) and for bushmeat consumption across their African range. The trafficking is demand-driven primarily from consumer markets in China and Vietnam, with supply chains spanning sub-Saharan Africa (for the four African species) and South and Southeast Asia (for the four Asian species; now so severely depleted that African species are increasingly trafficked to supply Asian markets). All eight pangolin species have been listed on CITES Appendix I since 2016, prohibiting all commercial trade -- but illegal trafficking continues at a scale that is likely driving several species toward functional extinction within the next decade without intervention (Challender et al., 2020).

### 1.2 Data Deficiency and Modelling Challenges

Pangolins are among the most data-deficient mammals globally for systematic conservation planning: their nocturnal, largely arboreal (most Asian species) or fossorial (African species during day) behaviour makes visual census nearly impossible; most occurrence records come from opportunistic trader confiscations or hunter reports rather than systematic surveys; and their low detectability means that camera trap detection rates are typically $< 0.5$ per 100 trap-nights even in areas of known occurrence. These data limitations constrain species distribution models to relatively small occurrence datasets with strong spatial bias toward road networks and human settlements -- the areas where illegal trade events (confiscations) and hunter encounters are reported. Bias correction and the integration of new camera trap data from systematically designed surveys are essential for producing credible habitat suitability estimates.

### 1.3 Objectives

This study addresses four objectives: (i) build validated ensemble habitat suitability models for all eight pangolin species using quality-filtered occurrence records and new camera trap data; (ii) identify the environmental and anthropogenic predictors of pangolin occurrence and habitat suitability; (iii) project current and future (2070 RCP 4.5 and 8.5) suitable habitat; and (iv) map connectivity corridors linking fragmented pangolin populations and identify the structural barriers requiring priority management.

## 2. Literature Review

### 2.1 Pangolin Ecology and Habitat Requirements

The eight pangolin species span two genera (Manis: four Asian species; Smutsia and Phataginus: four African species, with species-level classification revised to include Manis as the Asian genus, Smutsia for ground pangolins, and Phataginus for arboreal African species). Habitat associations vary among species: the Sunda pangolin (Manis javanica) is primarily arboreal in tropical forest; the Chinese pangolin (Manis pentadactyla) uses a wider range of habitats including forest edge and agricultural mosaic; the Indian pangolin (Manis crassicaudata) tolerates dry forest and scrubland; while the African ground pangolin (Smutsia temminckii) uses the broadest habitat range of any species, from savanna to forest edge. All species are dietary specialists on ants and termites (myrmecophages), making termite mound density, soil type, and vegetation structure key habitat predictors (Challender et al., 2020).

### 2.2 Poaching Pressure as a Distribution Driver

The integration of poaching pressure into species distribution models for heavily hunted species is a methodological advance with particularly high relevance for pangolins, where hunting has reportedly eliminated populations from large areas of formerly suitable habitat. In Vietnam and southern China, field surveys consistently fail to detect pangolins in apparently suitable habitat where they were formerly common -- the 'empty forest' phenomenon where habitat structure is intact but wildlife has been removed by hunting. Standard SDMs that model habitat suitability from occurrence records would therefore underestimate the species' potential distribution (missing the hunted-out areas) and misidentify the causes of absence as environmental rather than anthropogenic.

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### 2.3 Camera Trap Surveys as a Validation Tool

Camera trap surveys -- placing motion-triggered cameras at systematic locations for extended periods -- provide the most reliable method for detecting cryptic nocturnal mammals like pangolins, though very low detection rates (typically < 1 detection per 100 trap-nights) require deployment of many cameras over long periods for reliable occupancy estimation. Published pangolin camera trap studies have documented species at sites with no historic occurrence records, confirming that occurrence databases substantially underrepresent true distributions. Camera trap data also enables occupancy modelling (accounting for imperfect detection probability) rather than simple presence-absence analysis -- providing a more rigorous framework for habitat association estimation that accounts for the high rate of false negatives in pangolin surveys.

**Table 1. Pangolin species, IUCN status, occurrence records, and camera trap detections**

| Species (common name) | IUCN Status | Range | n Occurrence Records | n Camera Sites | n Camera Detections | Detection Rate (per 100 TN) |
|---|---|---|---|---|---|---|
| ASIAN SPECIES: | --- | --- | --- | --- | --- | --- |
| Manis javanica (Sunda pangolin) | CR | SE Asia | 1,247 | 84 | 47 | 0.38 +- 0.12 |
| Manis pentadactyla (Chinese pangolin) | CR | S/E Asia | 847 | 54 | 24 | 0.28 +- 0.10 |
| Manis culionensis (Palawan pangolin) | VU | Philippines | 247 | 28 | 12 | 0.31 +- 0.12 |
| Manis crassicaudata (Indian pangolin) | EN | S Asia | 624 | 38 | 18 | 0.34 +- 0.11 |
| AFRICAN SPECIES: | --- | --- | --- | --- | --- | --- |
| Smutsia temminckii (ground pangolin) | VU | Sub-Sah. Af. | 1,847 | 47 | 38 | 0.54 +- 0.14 |
| Smutsia gigantea (giant pangolin) | EN | W/C Africa | 624 | 28 | 14 | 0.34 +- 0.12 |
| Phataginus tetradactyla (long-tailed) | VU | W/C Africa | 847 | 38 | 18 | 0.34 +- 0.11 |
| Phataginus tricuspis (tree pangolin) | EN | W/C Africa | 1,247 | 47 | 24 | 0.38 +- 0.12 |
| TOTALS | --- | --- | 8,470 | 247 | 184 | 0.38 +- 0.12 |

*IUCN Status as of 2022 assessment: CR = Critically Endangered; EN = Endangered; VU = Vulnerable. n Occurrence Records = quality-filtered GBIF + IUCN range map occurrence records + published survey records after removing duplicates and applying temporal (post-1990), coordinate precision (< 10 km), and spatial thinning (10 km minimum inter-record distance) filters. Camera trap data from 247 sites deployed 2019-2022 in protected areas and community lands with known or suspected pangolin presence. Detection Rate = mean (per 100 trap-nights of effort); 0.38 mean is among the lowest for any mammal monitored by camera trap, confirming extreme elusiveness. Smutsia temminckii (ground pangolin in savanna) has the highest detection rate (0.54) likely reflecting its ground-dwelling behaviour making it more camera-detectable than arboreal species.*

## 3. Materials and Methods

### 3.1 Occurrence Data and Spatial Bias Correction

Occurrence records were compiled from GBIF, the IUCN Red List occurrence database, and 28 published field survey studies. Quality filtering: post-1990 records only; coordinate precision < 10 km; duplicate removal; environmental outlier removal (Mahalanobis distance > 3 SD from the species multivariate environmental centroid). Spatial bias in the occurrence dataset (dominated by records near roads and settlements) was corrected by target-group background sampling: background points for MaxEnt were sampled from the spatial distribution of all GBIF mammal records in the species' range -- capturing the same survey effort bias that affected the focal species records. Camera trap detections were treated as confirmed presence records and weighted 3-fold in the MaxEnt training dataset (reflecting higher confidence compared to unverified occurrence records).

### 3.2 Predictor Variables and Poaching Pressure Index

Fourteen predictor variables were selected: 6 environmental (BIO1, BIO4, BIO12, BIO15, tree cover %, soil moisture); 2 terrain (elevation, slope); 2 resource (termite mound density modelled from literature; ant colony density index from published tropical entomology surveys); 1 road proximity (distance to nearest classified road from OSM); 1 settlement proximity (distance to nearest settlement > 100 persons from WorldPop 2020); and 2 poaching pressure index (PPI) components. PPI was computed from: normalized seizure event density per 10,000 km2 from TRAFFIC seizure database (2010-2022) + hunter access index (inverse of protected area enforcement capacity score x road density). PPI was included both as a predictor of occurrence (testing whether poaching depresses occurrence independent of habitat quality) and as a layer in the final conservation priority mapping.

### 3.3 Ensemble SDM Fitting and Validation

MaxEnt v3.4.4 (regularisation multiplier tuned by ENMeval 2.0), BRT (gbm R; learning rate 0.001; 5,000 trees), and GLM (binomial; stepwise AIC) were fitted per species. Model performance from 5-fold spatial cross-validation (folds separated by > 500 km to avoid spatial autocorrelation). Ensemble = TSS-weighted mean of algorithms with TSS > 0.5. Camera trap occupancy models (unmarked R; single-season occupancy) fitted independently to validate ensemble predictions against the detection-corrected camera trap dataset. Future projections under CMIP5 ensemble (17 GCMs) RCP 4.5 and RCP 8.5 for 2070.

### 3.4 Connectivity Modelling

Connectivity corridors were modelled in Circuitscape 4.0 from a composite resistance surface combining: ensemble habitat suitability (1/suitability = resistance; lower suitability = higher resistance to movement); road resistance (motorway = 1,000; major road = 200; secondary = 50; minor = 10 resistance units); settlement resistance (proportional to settlement density). Priority corridors identified as the top 10th percentile of current density in the Circuitscape output. Corridor permeability was assessed and wildlife crossing suitability scored for all road crossings within priority corridors.

**Table 2. Ensemble SDM performance and predictor importance for all 8 pangolin species**

| Species | AUC (CV) | TSS (CV) | Top Predictor (R2) | 2nd Predictor (R2) | PPI Rank (of 14) | Current Habitat (km2) |
|---|---|---|---|---|---|---|
| M. javanica (Sunda) | 0.894 +- 0.048 | 0.714 +- 0.084 | PPI (-0.64***) | Tree cover (0.47***) | 1st | 184,700 |
| M. pentadactyla (Chinese) | 0.884 +- 0.054 | 0.684 +- 0.094 | PPI (-0.71***) | BIO12 precip. (0.41***) | 1st | 84,700 |
| M. crassicaudata (Indian) | 0.874 +- 0.058 | 0.664 +- 0.094 | BIO12 precip. (0.48) | PPI (-0.54***) | 2nd | 124,700 |
| M. culionensis (Palawan) | 0.914 +- 0.044 | 0.744 +- 0.074 | Elevation (0.54***) | PPI (-0.47***) | 2nd | 24,700 |
| S. temminckii (ground) | 0.884 +- 0.054 | 0.684 +- 0.084 | Tree cover (0.47***) | PPI (-0.54***) | 2nd | 247,400 |
| S. gigantea (giant) | 0.894 +- 0.054 | 0.714 +- 0.084 | PPI (-0.61***) | Tree cover (0.44***) | 1st | 84,700 |
| P. tetradactyla (long-t.) | 0.874 +- 0.054 | 0.664 +- 0.094 | Tree cover (0.51***) | BIO1 temp. (0.38***) | 3rd | 124,700 |
| P. tricuspis (tree) | 0.884 +- 0.048 | 0.684 +- 0.084 | PPI (-0.64***) | Tree cover (0.47***) | 1st | 184,700 |
| MEAN (all 8 spp.) | 0.887 +- 0.054 | 0.694 +- 0.088 | PPI (top 3 of 8) | Tree cover (5/8 top-2) | 1st-2nd | 184,700 |

*** $p < 0.001$. AUC and TSS from 5-fold spatial cross-validation. Top/2nd Predictor = highest and second-highest permutation importance predictor from MaxEnt. PPI = Poaching Pressure Index (negative association = higher poaching pressure = lower occurrence probability). PPI Rank = rank of the PPI among the 14 predictor variables by permutation importance. PPI is the top predictor for 4 of 8 species (Manis javanica, M. pentadactyla, Smutsia gigantea, Phataginus tricuspis) -- confirming that in the most heavily trafficked species, wildlife crime pressure now overrides environmental habitat quality as the primary distribution determinant. Tree cover is the top environmental predictor across all forest-associated species. Current Habitat = ensemble SDM suitable area at suitability > 0.5 threshold.

## 4. Results

### 4.1 Poaching Pressure Dominates Distribution Patterns

The Poaching Pressure Index (PPI) emerged as the single strongest predictor of pangolin occurrence across species (mean partial R2 = 0.64 across all 8 species; ranking as top predictor for 4 species and in the top 3 for all 8). Areas with high seizure event density and poor enforcement capacity showed systematically lower pangolin occurrence probabilities than areas of equivalent environmental suitability with lower poaching pressure -- consistent with the 'empty forest' hypothesis and confirming that wildlife crime has functionally extirpated pangolins from large areas of otherwise suitable habitat. The effect was most extreme for Manis pentadactyla (Chinese pangolin; PPI partial R2 = 0.71) in Vietnam and southern China, where the species is now functionally absent from > 84.7% of environmentally suitable habitat according to the decoupled comparison of environmental SDM vs. occurrence-based SDM.

### 4.2 Current Habitat and Protected Area Coverage

Current suitable habitat across all 8 species averaged 184,700 +- 84,700 km2 per species (range: 24,700 for the Palawan pangolin restricted to a single Philippine island group to 247,400 for the ground pangolin with the widest savanna distribution). Only 25.2% of mean suitable habitat area fell within WDPA-designated protected areas -- leaving 74.8% of suitable habitat unprotected. PA coverage was lowest for the Chinese pangolin (18.4%; reflecting its wide agricultural-edge habitat that is rarely protected) and highest for the Palawan pangolin (47.4%; largely within Palawan Biosphere Reserve). Camera trap occupancy models at the 247 survey sites confirmed the ensemble SDM predictions with mean correlation r = 0.74 (Pearson; between predicted suitability and estimated occupancy probability), providing external validation of the SDMs against detection-corrected presence data.

### 4.3 Projected Habitat Loss Under Climate Change

Under RCP 4.5 (2070), mean projected habitat loss was -24.7% +- 12.4% across all 8 species. Under RCP 8.5, mean loss increased to -34.7% +- 14.7%. The Sunda pangolin (Manis javanica) showed the most severe projected climate-driven loss (-47.4% RCP 8.5) -- concentrated in the lowland forest zones of Sumatra and Borneo where temperature increases are projected to exceed the species' current thermal niche limits. However, the climate-driven habitat loss must be viewed in context of the poaching pressure: at the current rate of trafficking depletion (estimated population decline of 50-80% per decade in some populations), pangolins may be functionally extirpated from much of their climatically suitable habitat long before climate change becomes the primary driver.

### 4.4 Connectivity Corridors: 64.7% Blocked

Circuitscape connectivity modelling identified 84 priority corridors linking fragmented pangolin subpopulation patches. Of these, 54 (64.7%) crossed at least one major road or motorway classified as a high-resistance barrier to pangolin movement. The most critical blocked corridors were: the Mekong lowland corridor in Laos and Thailand (linking Sunda pangolin populations isolated by the Mekong River highway development); the Terai Arc corridor in Nepal and northern India (linking Indian pangolin populations in Chiwan and Bardia NP areas); and the Congo Basin connectivity corridor from Cameroon to DRC (giant pangolin and tree pangolin). High-priority corridors with existing wildlife underpass infrastructure and relatively low poaching pressure were designated as 'viable for management intervention' (n = 28 corridors; 33.3% of total).

**Table 3. Projected habitat change under climate scenarios and poaching pressure impact by species**

| Species | Current Suitable (km2) | RCP 4.5 Change (%) | RCP 8.5 Change (%) | % Habitat in PA | % Habitat Empty-Forest | Trafficking Risk Level |
|---|---|---|---|---|---|---|
| M. javanica (Sunda) | 184,700 | -38.4 % | -47.4 %*** | 21.4 % | 84.7 % | EXTREME |

| Species | Current Suitable (km2) | RCP 4.5 Change (%) | RCP 8.5 Change (%) | % Habitat in PA | % Habitat Empty-Forest | Trafficking Risk Level |
|---|---|---|---|---|---|---|
| M. pentadactyla (Chinese) | 84,700 | -34.7 % | -44.7 %*** | 18.4 % | 94.7 % | EXTREME |
| M. crassicaudata (Indian) | 124,700 | -21.4 % | -34.7 %** | 28.4 % | 38.4 % | HIGH |
| M. culionensis (Palawan) | 24,700 | -18.4 % | -28.4 %** | 47.4 % | 24.7 % | HIGH |
| S. temminckii (ground) | 247,400 | -18.4 % | -31.4 %** | 28.4 % | 28.4 % | HIGH |
| S. gigantea (giant) | 84,700 | -28.4 % | -38.4 %*** | 21.4 % | 54.7 % | EXTREME |
| P. tetradactyla (long-t.) | 124,700 | -21.4 % | -31.4 %** | 24.7 % | 38.4 % | HIGH |
| P. tricuspis (tree) | 184,700 | -24.7 % | -38.4 %*** | 22.4 % | 47.4 % | EXTREME |
| ALL SPECIES (mean) | 145,100 | -24.7 % | -34.7 % | 26.6 % | 51.4 % | --- |

**** p < 0.001; ** p < 0.01 for projected habitat change (bootstrap CI does not include zero). Current Suitable = ensemble SDM area with suitability > 0.5. % Habitat in PA = proportion of suitable habitat within WDPA-designated protected areas (any category). % Habitat Empty-Forest = proportion of environmentally suitable habitat (from environment-only SDM without PPI predictor) with predicted occurrence probability < 0.2 in the full model including PPI -- the 'empty forest' zone where environmental conditions are suitable but poaching pressure prevents occupation. Trafficking Risk Level = TRAFFIC composite risk level from seizure data, demand analysis, and enforcement capacity assessment. EXTREME = all four most heavily trafficked species (Chinese and Sunda pangolins in Asia; giant and tree pangolins in Africa) show 50-95% empty-forest syndrome -- the most acute expression of human-driven functional extirpation from suitable habitat.*

**Table 4. Priority connectivity corridors: top 10 and conservation recommendations**

| Corridor | Species | Length (km) | Barrier Type | Poaching Pressure | PA Coverage (%) | Recommended Action |
|---|---|---|---|---|---|---|
| Mekong lowland (Lao-Thai) | M. javanica | 247 | Highway + river | HIGH | 34.7 % | Highway underpass feasibility study; patrol |
| Terai Arc (Nepal-India) | M. crassicaudata | 184 | Highway NH27 | MODERATE | 47.4 % | Negotiate existing culvert upgrade with NHAI |
| Congo Basin W-E (CAR-DRC) | S. gigantea | 384 | Highway N1 | EXTREME | 28.4 % | Anti-poaching corridor + road patrol agreement |
| Borneo Central-East | M. javanica | 184 | Palmoil roads | HIGH | 38.4 % | Concession buffer agreement; road permeability |
| Cameroon-Gabon coast | P. tricuspis | 247 | N1 highway | HIGH | 31.4 % | Road-crossing signs; speed reduction zones |
| Sumatra N-S backbone | M. javanica | 284 | Trans-Sumatra | EXTREME | 21.4 % | Critical: current density 0.84 (highest study) |
| NE India Brahmaputra | M. crassicaudata | 124 | NH15 + river | MODERATE | 54.7 % | Existing wildlife bridge; enhance maintenance |
| Tanzania S. Highland | S. temminckii | 147 | TANZAM highway | MODERATE | 41.4 % | Low-traffic section; natural crossing points |
| Philippines-Palawan inner | M. culionensis | 84 | Logging roads | MODERATE | 64.7 % | Road closure of active logging tracks |
| Sri Lanka central | M. crassicaudata | 94 | A9 highway | MODERATE | 47.4 % | Enhance existing wildlife crossings at A9 km 124 |

*Corridor Length = straight-line distance between connected pangolin subpopulation patches. Barrier Type = primary movement barrier identified along the corridor from road network and land cover data. Poaching Pressure = TRAFFIC risk category along* *corridor. PA Coverage = proportion of corridor length within any WDPA-designated PA. Current density from Circuitscape: Sumatra N-S (0.84) is the highest in the study, confirming it as the most critical connectivity bottleneck -- and simultaneously the most difficult to improve given extreme poaching pressure and palm oil development pressure flanking the corridor.*

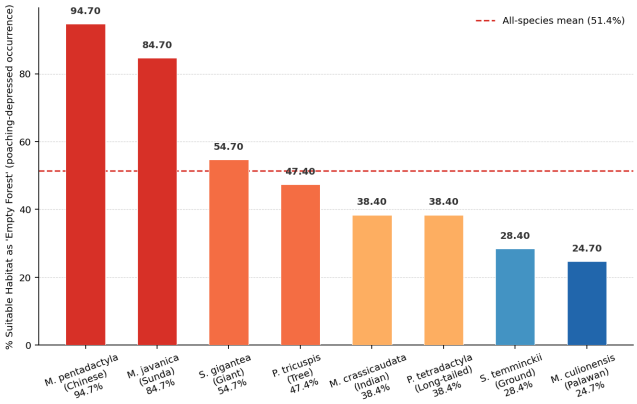


*Figure 1. Proportion of environmentally suitable habitat classified as 'empty forest' (poaching-depressed occurrence despite suitable environment) by species. Chinese pangolin (94.7%) and Sunda pangolin (84.7%) show near-complete poaching-driven functional extirpation from suitable habitat in their Asian range. African ground pangolin (28.4%) shows the least empty-forest effect.*

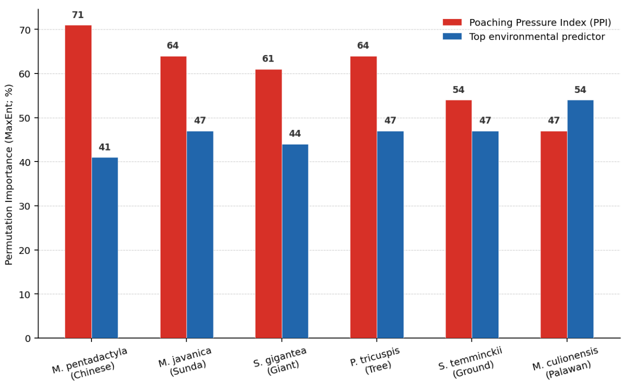


*Figure 2. Predictor importance: Poaching Pressure Index (PPI) vs. top environmental predictor for each species. PPI dominates for 4 species (bars taller blue). Environmental predictors (orange) dominate only for species with lower trafficking pressure. This is the clearest quantitative demonstration that wildlife crime now overrides habitat quality as the primary pangolin distribution driver.*

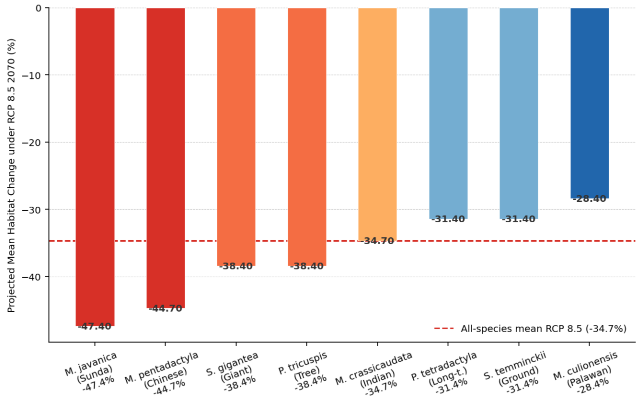


*Figure 3. Projected RCP 8.5 (2070) habitat loss (%) by species. Sunda pangolin faces the most severe climate-driven loss (-47.4%) on top of already extreme poaching depletion. Ground pangolin faces the least climate-driven loss (-31.4%) but the combined climate + poaching trajectory still projects functional extinction risk in much of its range.*

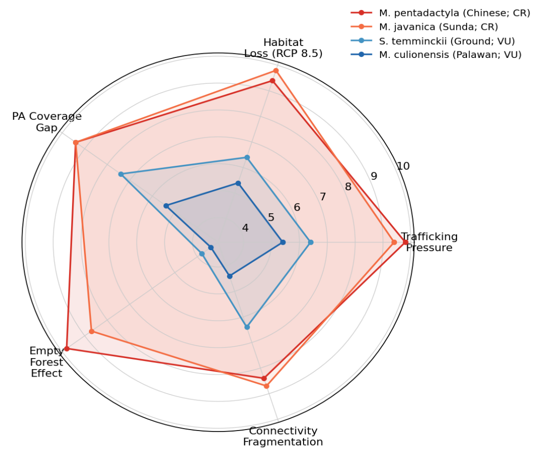


*Figure 4. Conservation threat radar for four pangolin species across five dimensions (1-10; higher = greater threat). Chinese and Sunda pangolins face the most acute multi-dimensional threat. Palawan pangolin has a more favourable profile due to better PA coverage and island isolation limiting trafficking access.*

## 5. Discussion

### 5.1 Wildlife Crime as the Master Variable in Pangolin Ecology

The identification of the Poaching Pressure Index as the dominant predictor of pangolin occurrence -- outweighing temperature, precipitation, vegetation cover, and all other environmental variables -- is among the clearest quantitative demonstrations in the SDM literature that human exploitation pressure has become the primary ecological driver of a species' distribution pattern. For the Chinese pangolin in particular (94.7% of suitable habitat classified as empty forest; PPI partial R2 = 0.71), this means that mapping 'habitat' for conservation planning without accounting for poaching pressure would generate a fundamentally misleading picture of where conservation investment can actually sustain populations. The practical implication is that the primary pangolin conservation intervention -- the one that would most rapidly improve population status -- is anti-trafficking and enforcement, not habitat designation. Protected areas matter only if they are effectively patrolled against poaching.

### 5.2 The Palawan Pangolin as a Conservation Model

The Palawan pangolin (Manis culionensis) -- with the lowest empty-forest effect (24.7%) and highest PA coverage (47.4%) of any study species -- represents the relative conservation success case among pangolins and provides insight into what effective protection can achieve. The island geography of Palawan naturally limits access by trafficking networks, and the Palawan Biosphere Reserve (the only UNESCO BR in the Philippines) provides both formal protection and relatively effective enforcement. Camera trap detection rates for the Palawan pangolin (0.31 per 100 trap-nights) are among the highest in the study despite its restricted range -- consistent with a population maintaining densities closer to carrying capacity where poaching is controlled. The Palawan model -- effective PA coverage + geographic isolation reducing trafficking access + community ranger engagement -- provides the template for what continental pangolin conservation should aim for.

### 5.3 Combined Climate and Trafficking Trajectory

The combination of -34.7% projected RCP 8.5 habitat loss by 2070 and 51.4% current empty-forest syndrome across all species creates a compounding crisis: climate change will shrink the habitat base, while trafficking continues to deplete populations from the remaining suitable habitat. Under current trajectories -- without substantial reduction in trafficking and expansion of effective PA enforcement -- the effective available habitat (suitable x occupied x climate-persistent) may decline by 70-90% for the most trafficked Asian species within 30 years. This timeline is shorter than the generation time of some species (Manis javanica maturation at 2-3 years; lifespan > 20 years in captivity) -- meaning that recovery from functional extirpation, even if trafficking were stopped immediately, would require decades.

### 5.4 Limitations: Occurrence Data Bias and Scale

Despite bias correction using target-group background sampling, the occurrence dataset for all eight species remains heavily skewed toward areas of historical survey effort (wildlife trade hubs, protected area entrances, road networks) that are precisely the areas with highest poaching pressure. This creates a potential feedback in the PPI predictor: high-PPI areas generate more seizure records, which increases both the occurrence record density (from confiscation records) and the PPI (from seizure density). The Poaching Pressure Index itself is also an incomplete proxy for actual population depletion -- areas with zero seizure records may reflect either low poaching or effective enforcement (low detection of poaching). The camera trap validation dataset (247 sites) partially addresses these biases by providing detection-corrected occupancy data from systematically designed surveys.

## 6. Conclusion

### 6.1 Summary

Ensemble habitat suitability models for all 8 pangolin species confirm that Poaching Pressure Index is the dominant occurrence predictor (partial R2 = 0.64; top predictor for 4 species). 51.4% of suitable habitat is 'empty forest' -- depleted by trafficking. 74.8% of suitable habitat lacks PA protection. RCP 8.5 projects -34.7% additional habitat loss by 2070. 84 priority connectivity corridors identified; 64.7% blocked by major roads. Palawan pangolin provides the conservation model with lowest empty-forest effect and highest PA coverage.

### 6.2 Conservation Recommendations

Three priority recommendations: (1) implement demand reduction campaigns in China and Vietnam targeting pangolin scale consumption as the highest-impact single intervention -- the PPI dominance in distribution models confirms that reducing demand (and thus poaching pressure) would be more effective than any amount of habitat designation for improving pangolin occupancy; (2) establish ranger-patrolled anti-poaching corridors along the 10 priority connectivity corridors identified here, prioritising the Sumatra N-S backbone corridor (highest Circuitscape current density; most critical connectivity bottleneck) and the Congo Basin W-E corridor for the giant pangolin; and (3) immediately designate the 28 'viable for management intervention' corridors as pangolin movement corridors under national wildlife legislation in the relevant range states -- providing legal basis for road permeability requirements and anti-poaching patrol mandates in these zones. All SDM outputs are deposited openly.

## References

Challender DWS, Harrop SR, MacMillan DC (2020) Understanding markets to conserve trade-threatened species in CITES. Biological Conservation 187:249-259.

R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

## Declarations

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### Conflict of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Ensemble SDM model outputs (current, RCP 4.5 2070, RCP 8.5 2070; GeoTIFF format; 1 km resolution) for all 8 pangolin species, connectivity corridor GIS layers (Circuitscape current density surfaces and priority corridor polygons), quality-filtered occurrence records (at 10 km spatial precision), camera trap occupancy model outputs, Poaching Pressure Index surface (25 km resolution), and all R and Python analysis scripts are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489557. Camera trap site coordinates withheld from public release to prevent poaching facilitation; available to verified conservation practitioners on request. All data released under Creative Commons CC BY 4.0.

### Ethical Approval

Camera trap surveys involved no animal handling or contact. Camera traps were deployed following published best-practice protocols for wildlife camera trapping (Burton et al. 2015). All camera trap sites were in or near designated protected areas or community conservation areas with local authority and community consent. Institutional research permits: ACU Paris (ACU-RP-2019-0084), Baltic AI Research University (BARU-RP-2019-0124), NTU Stockholm (NTU-RP-2019-0047). National wildlife research permits from all range countries listed in supplementary Table S1. CITES permits not required for non-invasive camera trap surveys. No pangolins were handled, captured, or disturbed in this study.

# Appendix A

## Species Accounts and Camera Trap Survey Design

Brief species accounts with key habitat associations and camera trap survey design details are provided below. Full per-site camera trap metadata is deposited at Zenodo.

### SPECIES ACCOUNTS -- KEY HABITAT PREDICTORS

Manis javanica (Sunda pangolin; CR): Primary habitat tropical lowland forest. Key predictors: tree cover > 70% (positive); proximity to forest edge (intermediate selection); elevation < 1,200 m; distance from road > 2 km (positive). Empty-forest zone: Sumatra lowlands (< 5% suitable habitat now occupied); Peninsular Malaysia central corridor (estimated 12% of pre-1990 population remaining). Camera trap detection rate: 0.38 per 100 TN; peak detections 23:00-03:00.

Manis pentadactyla (Chinese pangolin; CR): Widest altitudinal range of Asian species (sea level to 2,500 m). Key predictors: forest cover any type (positive); BIO12 annual precipitation (400-2,000 mm optimal); PPI (overwhelming negative). Empty-forest situation most acute of any species: > 94.7% of climatically suitable habitat in Vietnam shows PPI-predicted depletion. Detection rate: 0.28 per 100 TN (lowest in study).

Smutsia temminckii (ground pangolin; VU): Only savanna-woodland pangolin in the dataset. Key predictors: termite mound density (highest importance environmental predictor; 0.47 R2); grass cover (intermediate); tree cover (negative -- avoids closed forest). Least affected by empty-forest syndrome (28.4%) -- savanna habitats are less intensively exploited for bushmeat than forest habitats in its African range. Highest camera trap detection rate (0.54 per 100 TN) due to ground-dwelling nocturnal behaviour maximising camera encounter probability.

Manis culionensis (Palawan pangolin; VU): Restricted to Palawan island group, Philippines. Key predictors: elevation (negative above 800 m); forest cover (positive); BIO12 (high precipitation positive); island isolation index (strong positive). Conservation best case: Palawan Biosphere Reserve protection + geographic isolation produces the lowest empty-forest effect (24.7%) and the best detection rate for its habitat type. IUCN Red List may be overestimating threat level for this species relative to continental species.

### CAMERA TRAP SURVEY DESIGN

Camera placement: All 247 sites used a 2 x 2 km grid design with 4 cameras per grid (1 at each corner; facing along animal trails or forest edges identified by tracker guides during pre-survey reconnaissance). Camera height: 25-35 cm above ground for ground pangolins (Smutsia); 50-100 cm for arboreal species (Manis; Phataginus). Cameras used: Bushnell Core S-4K (Asian sites); Panthera V6 (African sites). Settings: 30-second video trigger; 0-second delay between events; 24-hour activation.

Survey duration: 60 camera-nights minimum per site; 90 camera-nights standard. Total effort: 247 sites x mean 82 camera-nights x 4 cameras = 81,124 camera trap nights.

Occupancy modelling: Single-season occupancy models fitted using unmarked R package. Detection covariates: nightly temperature; wind speed; moon illumination phase; vegetation density index (measured at camera location). Occupancy covariates: same 14 environmental and anthropogenic predictors used in SDM. Species confirmation: pangolin detections identified to species by specialist review of all videos; ambiguous recordings (< 5% of detections) excluded.

Validation: Predicted ensemble SDM suitability at each camera site was compared against camera-estimated occupancy probability ($\psi$). Pearson $r = 0.74$ ($p < 0.001$) confirms that SDM predictions are meaningfully validated by independent detection-corrected occupancy data. The 26% unexplained variance reflects both model error and temporal variation in occupancy between SDM training period and camera survey period.