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Modelling the conservation status of the threatened hoolock gibbon (genus *Hoolock*) over its range

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ABSTRACT

Habitat loss, degradation and fragmentation are major threats to all gibbon species, contributing to the dramatic decline of gibbons over the last 30–40 years. The Hoolock gibbon (genus Hoolock) in South and Southeast Asia, particularly those occurring between the Thanlwin River in the east and Brahmaputra River in the west, have been particularly impacted by these threats. We studied the extent of the remaining suitable habitat of hoolock gibbons over the species current range and identified stronghold areas for conserving remaining populations. Using logistic regression, we modelled the species presence in relation to a set of habitat variables and records to predict their probability of occurrence; threat levels were defined using a Bayesian Belief Network (BBN). Our results indicate the existence of approximately 199,447 km^2 of suitable habitats forming 27 strongholds for all three species of hoolock gibbon: the western hoolock (*Hoolock hoolock*), eastern hoolock (*H. leuconedys*) and Gaoligong hoolock (*H. tianxing*), with 18.9% of suitable habitats facing a high level of threat, 26.2% showing a medium threat level and 54.8% exhibiting a low level of threat. Our recommendations for the conservation of remaining populations include transboundary conservation between China and Myanmar, Myanmar and India, Myanmar and Bangladesh; introduction of population monitoring and conservation awareness programmes, translocation of scattered populations; and studies on the species status in strongholds with a high probability of occurrence, but with no species abundance information.

1. Introduction

Over recent decades, tropical forest biodiversity has collapsed (Butler and Laurance, 2008) due to high deforestation rates (Kim et al., 2015) following agricultural expansion (Pendrilla et al., 2019), unsustainable extraction of forest products (Henders et al., 2015), increased hunting pressure (Geissmann, 2007) and infrastructure development (Kim et al., 2015). Southeast Asia's tropical forest, grouped in four biodiversity hotspots and several species-rich ecoregions (Myers et al., 2000), is estimated to lose three-quarters of its original forests and half of its biodiversity by 2100 (Sodhi et al., 2004). At an annual forest loss increment of over 2100 km^2 in tropical Asia (from 2000 to 2012; Hansen et al., 2013), specialized large body species, particularly mammal populations, are losing their natural habitats at a fast speed (Srinivasulu and Srinivasulu, 2012) with an increased threat of extinction (ter-Steege et al., 2015). Among them, gibbons are a good example of mammals likely to face extinction in the near future (Pandit et al., 2007). Strictly arboreal and highly frugivorous, gibbons, one of the most threatened primate families, are closely associated with closed canopy broadleaved

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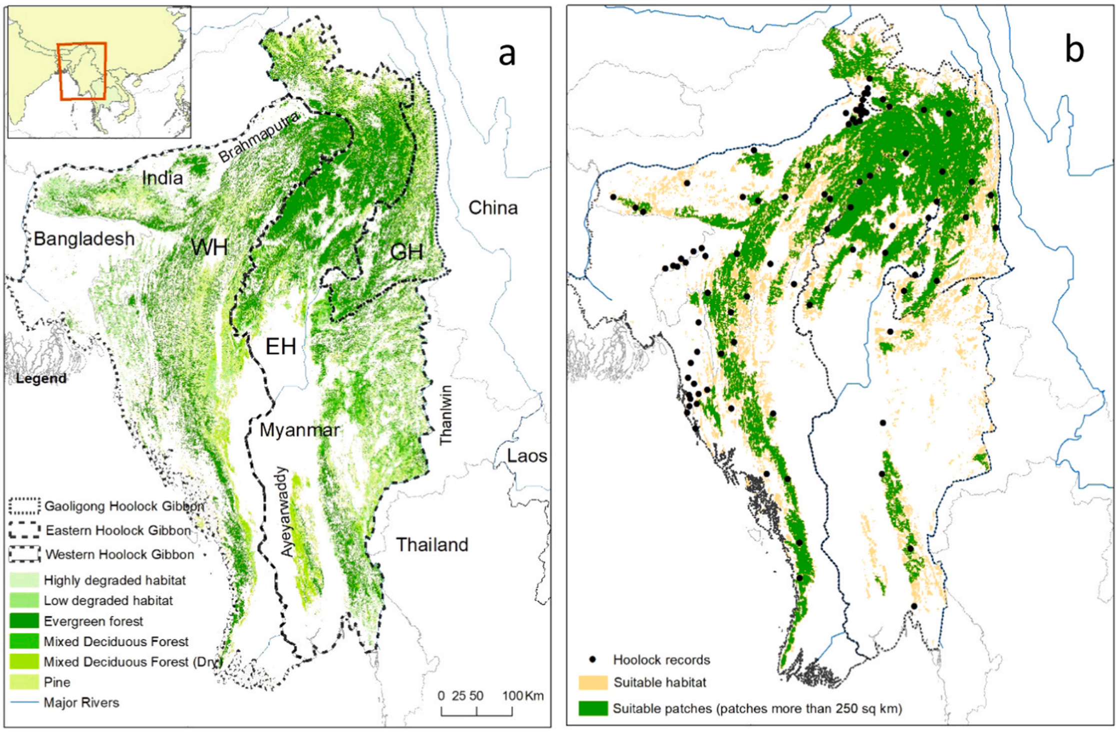

Fig. 1. (a) Forest cover map 2018 showing the distribution of three hoolock gibbons species, Gaoligong hoolock gibbon (GH), eastern hoolock gibbon (EH), and western hoolock gibbon (WH); (b) extension of suitable habitat with sites locations used in the analysis (see details of the 90 sites in Table S1).

evergreen pristine forests (Leighton, 1987) and respond poorly to habitat degradation and fragmentation (Arroyo-Rodriquez et al., 2013) with the repercussion that their populations have been in dramatic decline for the last 30–40 years (Cheyne et al., 2008).

Hoolock gibbons (genus *Hoolock*) inhabit the western part of the global distribution of gibbon (Fan et al., 2017), between the Thanlwin River in the east and the Brahmaputra River in the west (Chivers, 2013). The genus has three accepted species with a distribution centre in Myanmar, namely the western hoolock (*Hoolock hoolock*), also found in eastern Bangladesh, the eastern hoolock (*H. leuconedys*), also found in East India, and the newly described Gaoligong hoolock (*H. tianxing*), also found in China (Fan et al., 2017), delimiting their ranges with the Nmai Hka river, the Chindwin river and the Ayeyarwaddy river in Myanmar (Fan et al., 2017). Due to continuing population decline, as a consequence of habitat loss and fragmentation, two species (western and Gaoligong) are categorized as Endangered and the eastern hoolock as Vulnerable on the IUCN Red List (IUCN, 2019).

Hoolock gibbons inhabit a range of tropical foresta types, avoiding deciduous forest and scrub forest, mostly between 80 and 1500 m (Choudhury, 1996) with sporadic records up to 2550 m (Manipur, Northeast India, Choudhury, 2001). Despite their declining numbers, as a result of high hunting pressure and decreasing habitat, particularly in Myanmar where the third-largest pristine forest loss of 6.6% worldwide was recorded between 2005 and 2016 (Reddy et al., 2019), information on their status and habitat requirements at a landscape scale are poorly known, making conservation planning challenging. It is therefore imperative to understand the species distribution, the status of their remaining habitat and any associated threats (Engler et al., 2004) to establish effective conservation action plans (Tran et al., 2017).

Therefore, the aims of this study are to (1) estimate the extent of the remaining suitable habitat for hoolock gibbons within their known range and define how much of their suitable habitat has disappeared over the past 18 years using the species probability of occurrence, (2) define the major threats within the species range by combining forest loss hotspots and the distance to hunter access points in a Bayesian Belief Network (Petersen et al., 2020) and (3) define stronghold areas to initiate species monitoring programmes and provide recommendations for conserving remaining populations.

2. Study area

The study was conducted over the hoolock gibbons' entire range, including areas between the Thanlwin River in the east and Brahmaputra River in the west, with the species' ranges delimited by the NmaiHka River, Chindwin River and Ayeyarwaddy River in Myanmar (Fan et al., 2017) (Fig. 1a).

3. Methods

3.1. Probability of occurrence modelling

3.1.1. Species record locations

We obtained 687 species locations from both published information and records within www.gbif.org (https://doi.org/10.15468/dl.f2exd8), confirming the occurrence of hoolock gibbons from 1914 to 2019. We verified independence among the obtained locations by creating a 1 km radius circular plot at each location. When two circular plots overlapped for more than 5%, we selected only the one from the most recent record to represent the area occupied by the species. We derived a total of 414 independent locations (hereafter "locations"), which were used for habitat assessment to model the occurrence range. The 414 points are evenly distributed over the study area (see Fig. S1 for details). When several locations were located in the same area, within or outside protected areas, they were aggregated to represent individual sites. Locations were aggregated when more than one were found within the same forest patch and at a distance inferior to 35 km. In this case, the centre point between the aggregated locations was used to represent an area. Following the aggregation, we defined a total of 90 sites, seven for Gaoligong hoolock, 23 for eastern hoolock and 60 for western hoolock gibbons (for details on the sites see Table S1).

3.1.2. Habitat variables data

We first defined forest cover over the whole hoolock gibbons' range by combining forest cover maps for the year 2000 and 2018, obtained from Global Forest Change (https://earthenginepartners.appspot.com/science-2013-global forest/download_v1.6.html). We then defined habitat types for forest cover maps of 2000 and 2018 using the available habitat map for the year 2000, obtained from Climate Change Initiative Land Cover (CCI-LC) (http://maps.elie.ucl.ac.be/CCI/viewer/download.php). From the 34 original habitat types, we reclassified 12 habitat types to ensure compatibility with Southeast Asia land-cover types by comparing the resulting categories with geographical information system (GIS) data for each area to check for accuracy (Table S2 and Fig. 1a).

Second, we defined hoolock gibbons' suitable habitat using the probability of occurrence model. We collected 14 landscape variables: 1) altitude and slope, downloaded from Worldclim (www.worldclim.org), and 2) the other 12 habitat types derived above. Occurrence of gibbons will be varied on different forest types, altitude and slope (Tran and Vu, 2020).

Ultimately, we isolated only large patches of suitable habitat (hereafter "suitable patches"), for which we predicted the long-term survival (over 100 years), assuming 500 groups are required based on studies of other gibbon species (IUCN, 1994). At an average density of 2 groups/km^2, we estimated that a suitable patch needs to include a continuous forest block with a minimum size of 250 km^2.

3.1.3. Data analysis

Probability of occurrence models were constructed using an infinite weight logistic model (Hefley and Hooten, 2015) to investigate the relationship between given habitat covariates and the probability of occurrence from used versus available habitat selection models. A total of 414 used locations were derived based on presence-only data. Available locations, used to avoid the risk of using false absence locations, were generated from systematic random sampling by placing locations at 5-km intervals within used locations. Used and available locations were determined using clip and sampling tools in ArcGIS. A 1 km circular plot was created around each used and available location, and the altitude, slope and land-cover type were determined based on the 12 habitat types described above. Continuous variables were standardized, to transform the data to the same scale, by subtracting the mean from each value and dividing by the standard deviation (Gelman, 2008).

In total we compared 414 used locations with 19,933 available locations within a range polygon covering recorded locations (Fig. S2). Due to the imbalance dataset, in which presence points were much fewer than the available one, we used infinitely weighted logistic regression which reduces the effects of the imbalance on parameter estimates (Hefley and Hooten, 2015; Owen, 2007). The best model was selected using the lowest AIC. Statistical analyses were conducted using R Program 3.3.4 (R Development Core Team, 2019).

We created a square grid of 3.14 km^2 (standardized with the 1 km circular plots) covering hoolock gibbons' range and generated predictive maps of the probability of occurrence in each square grid based on the best model for the year 2000 and year 2018. In the end, we defined areas with more than 50% of probability of occurrence ($p > 0.5$) as suitable habitat for both predictive maps of the year 2000 and year 2018 (Fig. 1b).

3.2. Threats assessments

To define threats affecting the three hoolock gibbon species over their range, we used a Bayesian Belief Network (BBN), directed acyclic graphical model in which variables are represented as nodes and "parent nodes" impact the state of "child" nodes approach combining two nodes: forest loss hotspots and hunting level. Arcs link between parent nodes and child notes (Tantipisanuh et al., 2014), and the influence of the arcs to each node's state in the models are quantified using conditional probability tables (CPTs) (Bennett et al., 2021).

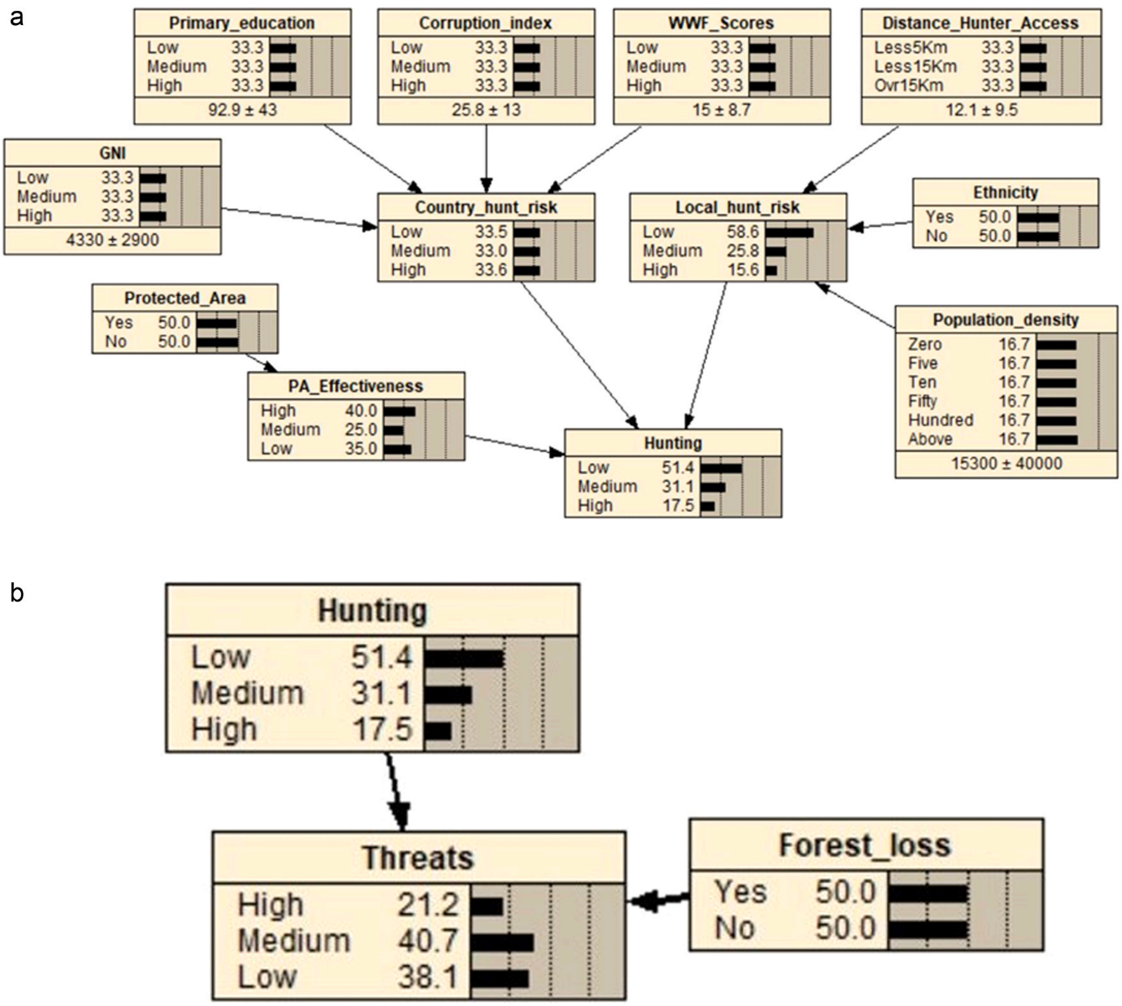

Fig. 2. (a). Bayesian Belief Network used to model the hunting level. Fig. 2(b). Bayesian Belief Network used to model Threat levels.

We used the map of forest loss hotspots from Petersen et al. (2020), generated using the Emerging Hot Spot Analysis tool in ArcGIS. The tool evaluates temporal changes in spatial clustering patterns to determine whether patterns are persistent, increasing, or decreasing over time. We used 30 m resolution annual forest loss raster data from 2000 to 2018 to investigate forest loss events over the entire species' range (see details of the Emerging Hot Spot Analysis in Peterson et al. (2020): Emerging hotspots of forest loss was identified using the Emerging Hot Spot Analysis geo-processing tool in ArcGIS PRO version 2.2.0 (Environmental Systems Research Institute, 2018), following Harris et al. (2017). First identify statistically significant spatial clustering patterns of forest loss by conducting a traditional hotspot analysis using the Getis-Ord Gi* statistic (Ord and Getis, 1995) to apply annual forest loss data. After spatial clustering patterns are identified, it is determined whether patterns are persistent, increasing, or decreasing over time by evaluates temporal changes in those patterns using a Mann-Kendall test (Mann, 1945; Kendall and Gibbons, 1990)). By default, the Emerging Hot Spot Analysis tool categorizes each forest loss event into one of 17 distinct spatio-temporal categories (i.e. 1 non-significant category, 8 hotspot categories, and 8 cold spot categories). As we are interested in forest loss over the study period, we considered only hotspot categories. We divided hotspots into Intensifying Hotspots, referring to hotspots where the intensity of clustering of high counts in each time step is increasing; Persistent Hotspots, defined as those with no discernible trends indicating an increase or decrease in the intensity of clustering over time; and Sporadic Hotspots, defined as an on-again then off-again hotspot (Harris et al., 2017).

To define the hunting level, we used a Bayesian Belief Network model adapted from the model generated by Grainger et al. (2018),

Table 1
Parameters that influence the probability of occurrence model.

Parameters	β	SE	95%LCI	95%UCI
Altitude	-0.0004968	0.00009457	-0.000686518	-0.00032
Less Disturbance Habitat	-0.9072	0.2498	-1.431724	-0.45031
Evergreen Forest	0.1922	0.04364	0.1065923	0.277761
Mixed Deciduous Forest	-0.9746	0.2823	-1.57896	-0.46819

Table 2
Remaining habitat for the three species, and suitable habitat and suitable patches loss between 2000 and 2018.

Species	Suitable habitat in 2000 (km^2)	Suitable patches in 2000 (km^2)	Suitable habitat in 2018 (km^2) (Yellow in Fig. 1b)	Suitable patches in 2018 (km^2) (Green in Fig. 1b)	Suitable habitat loss between 2000 and 2018 (km^2)	Suitable patches loss between 2000 and 2018 (km^2)
western hoolock	92,620	78,132	88,256	73,878	3572	4254
eastern hoolock	90,468	78,092	89,047	75,459	2211	2633
Gaoligong hoolock	22,570	16853	22,142	16,343	428	510
All three species	205,658	173,076	199,447	165,679	6212	7396

by including one more node of Ethnicity based on our experience with biodiversity conservation issues in the study area (Fig. 2a). Hunting level is conditional from local hunting risk, country hunting risk, and protected area effectiveness. Local hunting risk node was created under conditional of human population density (derived from CIESIN and CIAT, 2005), distance to hunting access (estimated by the location of roads to forest edge, data derived from CIESIN and ITOS, 2013), and ethnicity. Risk from ethnicity was categorised from ethnicity distribution followed the state and region of each country (data derived from https://diva-gis.org/gdata) and gibbon hunting status in the different ethnic group's areas that were extracted from published information (Choudhury, 2006; Islam et al., 2006; Fan et al., 2011; Geissmann et al., 2013). At country level, a country hunting risk node was created under conditional information from the WWF Wildlife Crime Score (Nowell, 2012), Corruption Index (http://www.transparency.org/), percentage of primary education and gross national income (http://data.worldbank.org/). The conditional probability tables (CPT; see Tables S3, S4 and S5) defined three categories of hunting level: high, medium and low.

In the end, we defined threat levels by combining, on a second Bayesian Belief Network model, two nodes: the forest loss hotspot from Peterson et al. (2020) and hunting level from first BBN, and the output produced three levels of threat: high, medium and low applied on a 1×1 km^2 scale grid over the whole species' range.; Fig. 2b). The conditional probability tables (CPT; see Table S6) defined three categories of threat: high, medium and low.

3.3. Protection assessment

To investigate the extent of protection of suitable patches, we overlaid the protected area boundaries layer (downloaded from www.protectedplanet.net) over suitable patches layer.

3.4. Defining management strongholds

Management Strongholds were defined based on the presence of large contiguous habitat patches showing a probability of occurrence for the genus higher than 50% ($p > 0.5$), as recorded for 2018. Strongholds were classified into three categories based on the recorded status of the presence/absence of gibbons: 1) Confirmed Presence Strongholds, where the species presence is confirmed using the data collected from GBIF Occurrence as well as those found in published references, for China; Chan et al. (2017), Fan et al. (2011); for Myanmar: Brockelman et al. (2009), FFI (2012), Geissmann et al. (2013), Groves (1972), Jenkins (1990), Kingdon Ward (1949), Lwin et al. (2021), Lynam (2003), Morris (1936), Riley and Shortridge (1913), WCS (2015); for India: Chetry and Chetry (2010), Chetry et al. (2010), Choudhury (2006, 2013), Das et al. (2006), Kakati et al. (2009), Islam et al. (2013), Pachuau et al. (2013), Ray et al. (2015), and for Bangladesh: Islam et al. (2006) (see Table S1 for details), 2) Absence Strongholds, where the presence of the species was not confirmed despite undertaken surveys in 2018 and 2019 by WWF (WWF, 2020), and 3) Expected Presence Strongholds, where there are no survey data confirming the species presence or absence.

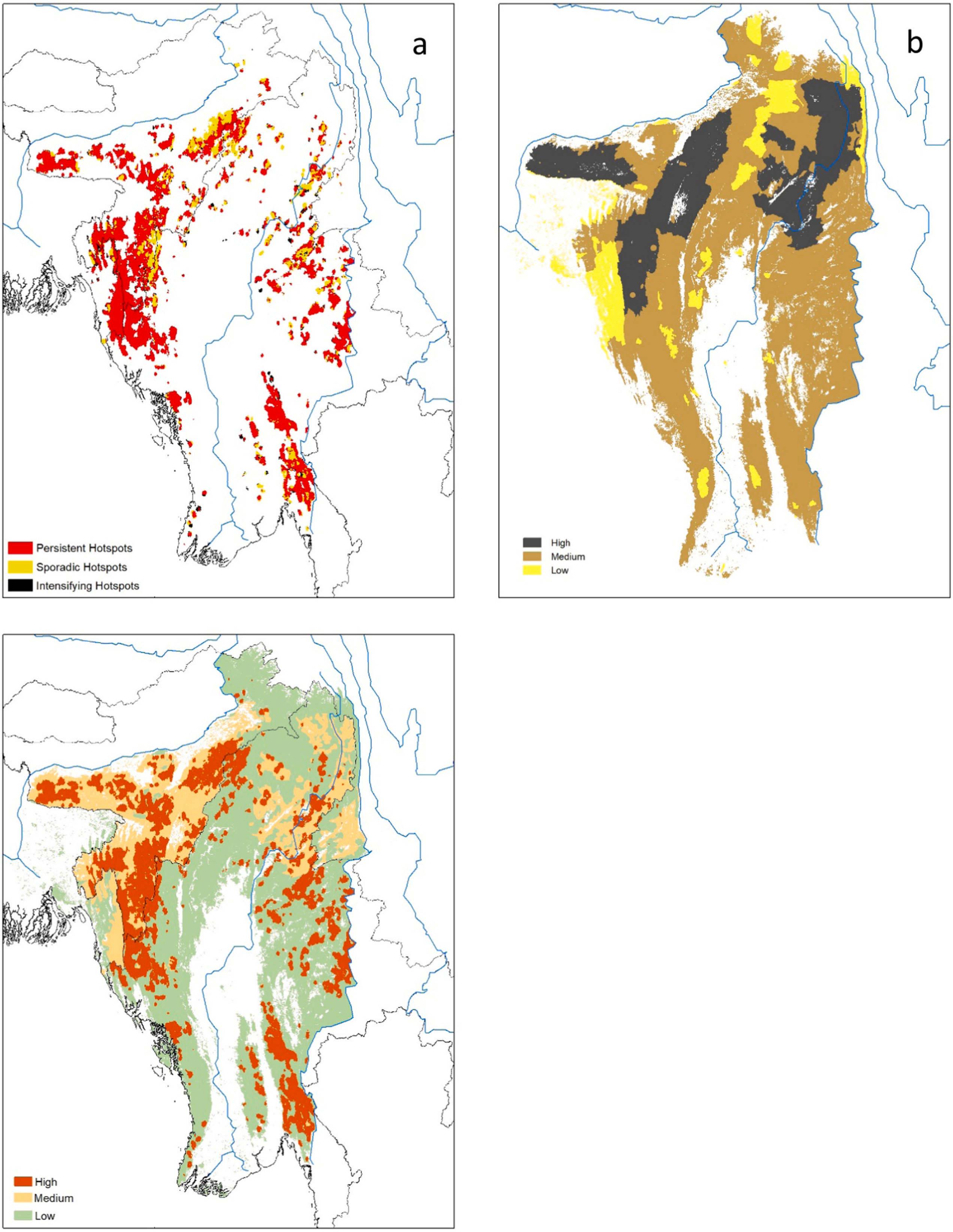

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Fig. 3. (a)Forest loss hotspots defined between 2000 and 2018, b) hunting level map, and (c) combined threat level over the hoolock gibbons range obtained using BBN.

Table 3
Threat level of suitable patches of each species and area of suitable patches inside protected area.

Species	High level	Medium level	Low level	Inside protected areas
western hoolock	35% (26,195 km2)	22% (16,614 km2)	42% (31,069 km2)	16% (11,866 km2)
Eastern hoolock	10% (7644 km2)	18% (13,457 km2)	72% (54,357 km2)	28% (20,763 km2)
Gaoligong hoolock	14% (2242 km2)	55% (8933 km2)	32% (5167 km2)	5% (861 km2)

4. Results

4.1. Forest cover and suitable habitat

Forest cover over the hoolock gibbons' range was 422,174 km^2, with 189,358 km^2 for the western hoolock, 196,497 km^2 for eastern hoolock and 36,319 km^2 for Gaoligong hoolock (Fig. 1a).

The best model defining suitable habitat (AICc=11522) included elevation, evergreen forest, less disturbance forest and mixed deciduous forest (Appendix Table 1). The model showed that the probability of occurrence was positively influenced by evergreen forest but was negatively influenced by the elevation, less disturbance forest and mixed deciduous forest (Table 1). Details on remaining habitat for the three species are in Table 2.

4.2. Threats

Forest loss hotspots covered a total area of 135,021 km^2 with 5095 km^2 for New or Intensifying Hotspots, 102,903 km^2 for Persistent Hotspots and 27,022 km^2 for Sporadic Hotspots (Petersen et al., 2020; Fig. 3a).

Results of the hunting level assessment with BBN suggested that 28.8% of the total forest area in the hoolock gibbons' range had high hunting probability, 60% had medium hunting probability and 11.2% had low hunting probability (Fig. 3b). Areas with high hunting pressure were mostly in India and Northern Myanmar, while low hunting areas were in Bangladesh and protected areas in all four countries.

Results of the threat assessment (Fig. 3c) reveals that 19% of suitable habitat (37,722 km^2) faces a high threat level, 26% (52,383 km^2) exhibits a medium threat level, and 55% (109,342 km^2) shows a low threat level. A total of 36,692 km^2 of suitable habitat falls within protected areas.

The threat assessment also shows that 22% of suitable patches (36,090 km^2) face a high threat level, 23.5% (39,004 km^2) face a medium threat level, and 55% (90,593 km^2) exhibits a low threat level. Overall, only 33,490 km^2 (25%) of suitable patches are located in protected areas (Fig. S3).

Details on the threat level of suitable habitat and suitable patches of each species are in Table 3.

4.3. Strongholds

We defined a total of 27 strongholds (see Table 4 for details) with 14 Confirmed Presence strongholds, one Absence stronghold and 12 Expected Presence strongholds (Fig. 4a). For the western hoolock gibbon, 11 strongholds were defined, six where the presence was confirmed (numbers 2, 6, 10, 11, 23 and 24) and five where the presence was expected (numbers 12, 15, 16, 21 and 22). For the eastern hoolock gibbon, a total of 14 strongholds were defined, seven in which the species presence was confirmed (numbers 1,3,7, 8, 9, 13 and 25), six with expected species presence (numbers 14, 17, 18, 19, 20 and 26) and one where the species was absent (number 27). Meanwhile for the Gaoligong hoolock gibbon, two Confirmed Presence strongholds were found (numbers 4 and 5).

The results showed that 21% (32,029 km^2) of Confirmed Presence strongholds had a high threat level, 24% (36,128 km^2) faced a medium threat level, while 54% (81,565 km^2) faced a low threat level, with an area of 33,350 km^2 protected. For Expected Presence strongholds, 26% (4025 km^2) had a high threat level, 18% (2876 km^2) faced a medium threat level, while 56% (8749 km^2) faced a low threat level, and only 1% (140 km^2) of the area was protected. Meanwhile, 10% (27 km^2) of Absence strongholds showed a high threat level, and 91% (277 km^2) showed a low threat level; the Absence strongholds showed no medium threat level nor fell within protected areas (Fig. 4b).

Table 4

Details of the 27 Strongholds regarding the area of suitable patches, overlap with protected areas, threat levels, densities and site numbers. GH = Gaoligong hoolock gibbon, EH = eastern hoolock gibbon, WH = western hoolock gibbon For site details, see Table S1.

Strongholds No.	Species	Total sites	Site numbers	Sites with population estimated			Suitable patches (km2)	Threats level (km2)			Protected Area (km2)	Strongholds class
				No. of sites with density	Density (group/km2)	No. of groups count		High	Medium	Low		
1	EH	3	1, 5, 8	3	2.4	206	12870.4	285.3	441	12,144.2	3636.3	Confirmed Presence
2	WH	9	17, 18, 19, 20, 23, 25, 27, 30, 32	1	1.27	39	25,412.1	7496.8	4070	13,845.3	8757.2	Confirmed Presence
3	EH	5	9, 13, 21, 24, 33	4	1.3–2.23	NA	30,883.3	1677.4	7385.8	21,820.1	11,909.4	Confirmed Presence
4	GH	3	26, 58, 60	1	0.98	NA	13,039.9	2086.3	8051.3	2902.3	613.2	Confirmed Presence
5	GH	3	29, 38, 43	NA	NA	34	3302.7	156	882.1	2264.6	247.4	Confirmed Presence
6	WH	1	22	NA	NA	NA	2263.9	734.6	1312.3	217.1	21.5	Confirmed Presence
7	EH	1	36	1	1.36	NA	11,207.1	663.6	2113.9	8429.7	4830.5	Confirmed Presence
8	EH	0		NA	NA	NA	4347.3	175.1	1041.4	3130.8	96.8	Expected Presence
9	EH	1	46	1	2.07	NA	4297.8	222.6	2475.4	1599.8		Confirmed Presence
10	WH	2	40, 41	NA	NA	120	1024.4	591.2	433	0.3	21.5	Confirmed Presence
11	WH	8	31,35,49,61,62,64,67,69	NA	NA	209	20,385.4	11,109.6	8463.6	812.2	1248	Confirmed Presence
12	WH	0		0	0	0	2462.1	538.8	678.6	1244.8		Expected Presence
13	EH	1	63	1	2.3	NA	3031.3	32.3	0	2999.1	290.5	Confirmed Presence
14	EH	0		0	0	0	379.5	13.8	0	365.8		Expected Presence
15	WH	0		0	0	0	291.4	88.1	203.4	0		Expected Presence
16	WH	0		0	0	0	1352.9	140.8	429.3	782.8		Expected Presence
17	EH	0		0	0	0	294.5	0	0	294.5		Expected Presence
18	EH	0		0	0	0	660.2	571.1	0	89.1		Expected Presence
19	EH	0		0	0	0	370.1	133.4	0	236.7		Expected Presence
20	EH	0		0	0	0	566.3	131.6	0	434.8		Expected Presence
21	WH	0		0	0	0	460.8	0	98.9	361.9	43	Expected Presence
22	WH	0		0	0	0	3937	2232.8	424.7	1279.5		Expected Presence
23	WH	1	77	NA	NA	NA	1570.3	504.4	452.6	613.3		Confirmed Presence
24	WH	4	80, 86, 87, 89	4	0.32–2	NA	14,717.8	2758.4	47.2	11,912.2	1775.1	Confirmed Presence
25	EH	2	84, 88	1	0.5	NA	5716.8	3711.3	0	2005.5		Confirmed Presence
26	EH	0		0	0	0	528.9	0	0	528.9		Expected Presence
27	EH	0		0	0	0	305	27.2	0	277.8		Absence

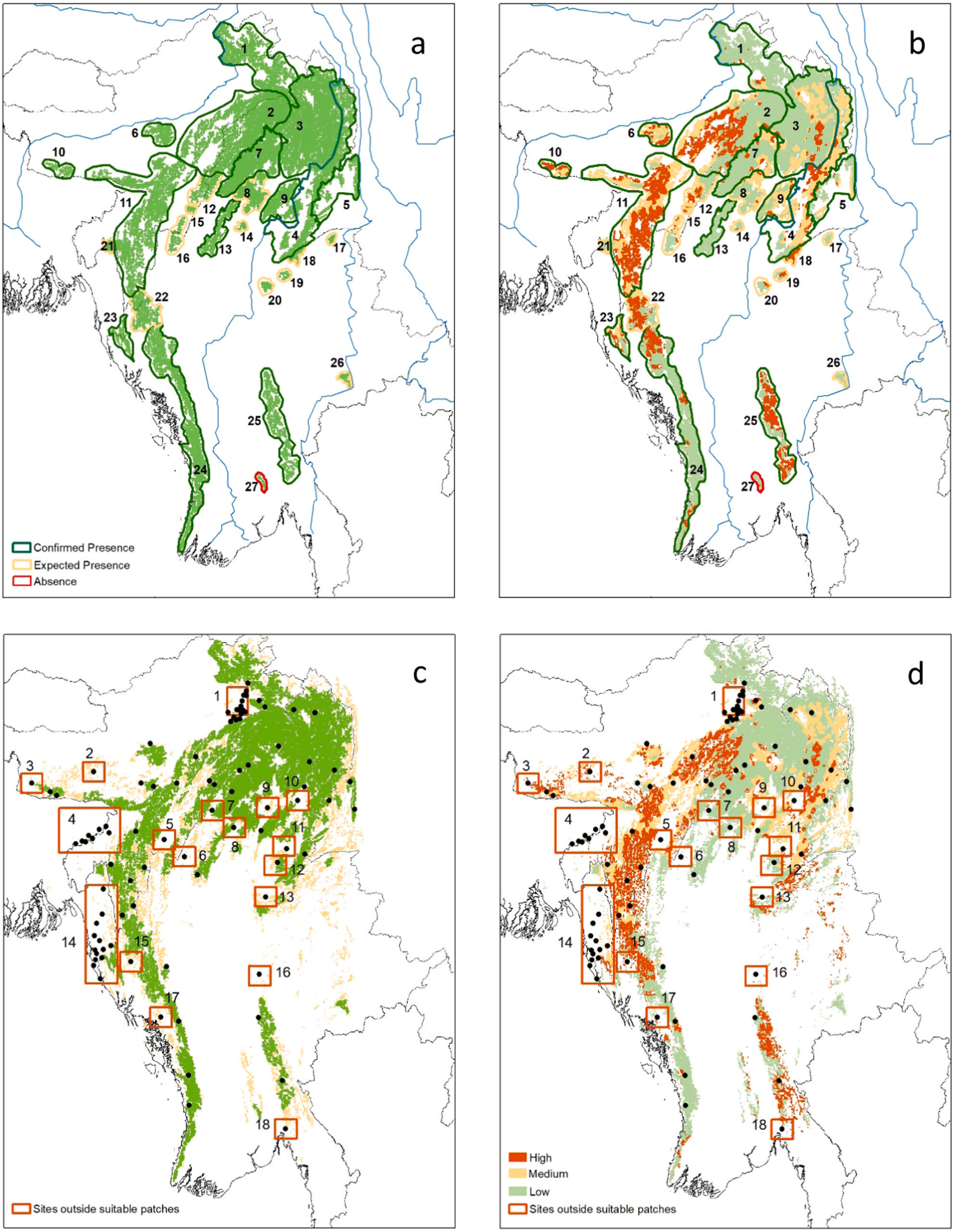

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Fig. 4. (a) Map showing class of stronghold areas; (b) threat levels in stronghold areas; (c) map of sites outside the suitable areas; (d) threat levels of areas occupied by gibbons outside the strongholds.

Table 5
Suitable sites outside the strongholds.

Highlighted Areas No.	Total No. of sites	Record Year	No. of sites with density	Density (group/km2)	No. of groups count	Site numbers	Species
1	11	2002, 2010	2	0.65	44	2,3,4,6,7,10,11,12,14,15,16	WH
2	1	2005	NA	NA	20	28	WH
3	1	2005	NA	NA	20	37	WH
4	8	2002, 2012	NA	NA	31	47,48,50,51,53,54,55,57	WH
5	1	2001	NA	NA	50	52	WH
6	1	1960	NA	NA	NA	59	WH
7	1	1935	NA	NA	NA	44	EH
8	1	2000	NA	NA	NA	45	EH
9	1	2019	1	4.64	NA	42	EH
10	1	1937	NA	NA	NA	39	EH
11	1	1879	NA	NA	NA	56	EH
12	1	2000	NA	NA	NA	60	GH
13	1	1913	NA	NA	NA	66	EH
14	12	1997, 2002	NA	NA	60	65, 68, 70, 71, 72, 73, 74, 75, 76, 78, 81, 83	WH
15	1	2010	NA	0.32	NA	79	WH
16	1	1985	NA	NA	NA	82	EH
17	1	2009	NA	NA	NA	85	WH
18	1	1980	NA	NA	NA	90	EH

We also highlighted 18 areas (hereafter "highlight areas"), including 46 sites (Table 5), where gibbon species have been detected, but their suitable habitat has now disappeared, or has reduced below the 250 km^2 limit that guarantees the long-term population survival (Fig. 4c). Fifteen highlight areas (numbers 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17, 18) consist of one site each, highlight area 1 consists of eleven sites, highlight area 4 has eight sites, and highlight area 14 holds 12 sites. Nine highlight areas were found in the western hoolock range, eight highlight areas occurred in the eastern hoolock range and one highlight area was found in the Gaoligong hoolock range.

In the end, we assessed the threat level in the highlight areas. Of 15 highlight areas containing one site each, four highlight areas (numbers 3, 2, 5, 18) showed a high threat level, three (number 9, 10, 11) showed a medium level and seven (numbers 6,7,8,12,13, 16, 17) showed a low level threat. Highlight area 1 with eleven sites and highlight area 14 with twelve sites both exhibited medium threat levels. Highlight area 4, which has eight sites, had a low level threat (Fig. 4d).

5. Discussion

Our model predicted a total of 199,447 km^2 of suitable hoolock gibbon habitat over their distribution range, with 165,679 km^2 represented by suitable patches, large enough to guarantee the long-term survival of the populations present. Between 2000 and 2018, 6212 km^2 of suitable habitat disappeared, resulting in a loss of 7396 km^2 of suitable patches. The estimated population density for the genus ranged between 0.02 and 4.64 groups/km^2. The estimated density recorded in India is between 0.08 and 1.15 group/km^2 (Choudhury, 2006), with figures between 0.02 and 0.8 group/km^2 reported in Bangladesh (Islam et al., 2006), 0.13–4.64 group/km^2 reported in Myanmar (Lwin et al., 2021) and 0.18–0.21 group/km^2 reported in China (Chan et al., 2017).

The western hoolock range covers about 45% of the whole hoolock gibbons' suitable habitat and showed the largest decline (58%) since 2000, mainly due to expending agriculture land in India and Myanmar (Pachuau et al., 2013; Geissmann et al., 2013). Large portions of the western hoolock suitable habitat were found in India, where the survival of the species is threatened by confirmed forest loss and fragmentation, resulting in an estimated population density ranging between 0.08 and 1.15 groups/km^2 (Choudhury, 2006), and in Bangladesh, where they are surviving in small pockets of fragmented forests with an estimated density between 0.02 and

0.08 km^2 (Islam et al., 2006). In Myanmar, the status of the species could be considered stable owing to the large continuous suitable habitat mostly showing a low level of threat (see Fig. 3c), however, few pockets of high threat are found is some areas, resulting in a population density ranging between 0.32 and 2 groups/km^2 (Geissmann et al., 2013).

Being mostly distributed in Myanmar and covering 44% of the whole hoolock gibbons' range, the eastern hoolock showed the largest extension of both large suitable habitat and suitable patches, which have declined by 36% since 2000 due to shifting cultivation practiced by the local communities and largescale timber extraction (Geissmann et al., 2013) as most of the remaining habitat is unprotected, with only 25% of suitable habitat falling within protected areas. The overall population density is estimated to range between 0.6 and 4.64 groups/km^2 in Myanmar with lower population density occurring outside protected areas, due to higher levels of threat, and higher population density occurring in the Indawgyi Biosphere Reserve (Lwin et al., 2021). In northern India, the species density was estimated at 0.65 groups/km^2 (Chetry et al., 2012).

Smaller amounts of both suitable habitat and suitable patches were recorded for the newly described Gaoligong hoolock (Fan et al., 2017); its range spans the border between China and Myanmar, covering 11% of the whole hoolock gibbons' suitable habitat, with only a 7% decline recorded since 2000. The species shows an overall small population with 200 individuals confirmed in China, but the current status in Myanmar is unknown (Chan et al., 2017). The remaining suitable habitat of Gaoligong hoolock is in isolated forest areas in China (Chan et al., 2017); and larger areas in Myanmar.

6. Strongholds

From the total estimate of 27 strongholds, highlighted over the hoolock gibbons' range, 11 strongholds were defined for the western hoolock. This species can be found in Myanmar, India and Bangladesh and show the largest remaining suitable habitat among the three species. However, 35% of the suitable habitat is classified as facing a high threat level. India has three Confirmed Presence strongholds (6, 10 and 11) with estimated populations of 120 groups in stronghold 10 (Choudhury, 2006) and 209 groups in stronghold 11 (Choudhury, 2006; Islam et al., 2013). There are no data for stronghold 6. Among them, strongholds 10 and 11 are under a high level of threat, with 58% and 54% of their areas respectively affected. Around 58% of the area in stronghold 6 faces a medium level of threat. Legal protection is highly limited, with only 2%, 6% and 1% of strongholds 10, 11 and 6 respectively covered. Choudhury (2006) reported high forest fragmentation primarily as a consequence of slash-and-burn shifting cultivation outside protected areas in strongholds 10 and 11, resulting in the decline of gibbon populations in this area. The status of stronghold 6 is unreported.

In Bangladesh, only one Expected Presence stronghold (number 21) was found to be contiguous to the Confirmed Presence stronghold number 11 in India, for which a relatively high number of groups was estimated despite its high threat level and limited legal protection. Confirmed Presence stronghold number 23, a transboundary stronghold between Myanmar and, to a limited extent, Bangladesh faces a medium level of threat.

In Myanmar, the estimated density of Confirmed Presence stronghold 24 was reported to range between 0.32 and 2 groups/km^2 (Geissmann et al., 2013; Myers et al., 2019); 12% of this area falls inside protected areas, and 81% of its area is under a low level of threat. No hunting was recorded, although forest habitat around villages has been lost as a result of shifting cultivation, therefore the gibbon population in remaining forests away from villages face no threat (Myers et al., 2019). Five transboundary Confirmed Presence strongholds (strongholds 2, 12, 16, 22 and 23) between Myanmar, India and Bangladesh were identified. With a reported density of 1.27 groups/km^2 (Geissmann et al., 2013), stronghold 2 is the largest stronghold for the species and shows a low level of threat (54%) with low human disturbance, most likely because 34% of its area falls within protected areas. Strongholds 12, 16 and 23 also show low levels of threat (51%, 58% and 39%, respectively), while 57% of the area in stronghold 22 is under a high level of threat. These strongholds do not overlap with protected areas.

A total of 14 strongholds were highlighted in the eastern hoolock range, one in India and 13 in Myanmar. The species presence was confirmed for the Indian stronghold (number 1), with an estimated population of 206 groups and an extremely low threat level (95% of the area), owing to the absence of hunting due to traditional beliefs; however, the traditional slash and burn agricultural practice still poses a threat (Chetry et al., 2010). Of the 13 Burmese strongholds, the species presence was confirmed in five (numbers 3, 7, 9, 13 and 25), with the estimated density ranging between 0.5 and 2.4 groups/km^2 at an average of 1.5 (WCS, 2015; Geissmann et al., 2013; Brockelman et at, 2009; Lynam, 2003; FFI, 2012). The strongholds mostly show a low threat risk (67% of the whole area), with 34% of them falling within protected areas. Only 11% of the combined area shows a high threat level, which can be linked to high hunting pressure and illegal logging (Geissmann et al., 2013). Stronghold 3 is the largest with an estimated density of 1.3–2.23 groups/km^2 and mostly exhibited a low level of threat (71%). Strongholds 7 and 9 have density estimates of 1.36 and 2.07 groups/km^2, respectively. Stronghold 7 faces a low threat level in 75% of its area, while stronghold 9 exhibits a medium threat level in 58% of its area. Overall, stronghold 13 is under a low threat level, whereas stronghold 25 shows a high threat level (65% of its area), which might explain the low density estimate of 0.5 group/km^2 (Geissmann et al., 2013). However, a high density of 4.6 groups/km^2 was recorded at Indawgyi Biosphere Reserve (Lwin et al., 2021). Geissmann et al. (2013) reported the reallocation of lowland villages affected by civil war to upland gibbon habitat, which has huge implications for the natural forest. Seven Expected Presence strongholds (numbers 8, 14, 17, 18, 19, 20 and 26) were identified within the 13 Burmese strongholds. While 87% of the area in stronghold 18 faces a high threat level, strongholds 8, 14, 17, 19, 20 and 26 mostly show a low threat level (72%, 96%, 100%, 64%, 77% and 100%, respectively). One Absence stronghold (number 27) was recently reported following extensive surveys (WWF, 2020), which could be linked to high human disturbance and hunting pressure in the past as the area has a long history of commercial timber extraction.

Ultimately, two Confirmed Presence strongholds (4 and 5) were identified in the Gaoligong hoolock range. Stronghold 5, located in China, has a population estimate of 40–43 groups (0.4 groups/km^2) within the Gaoligongshan Nature Reserve and has been considered stable in past surveys, with healthy reproduction both within and outside the surveyed areas (Fan et al., 2011). Stronghold 4, which is located in Myanmar, has an estimated density of 0.98 groups/km^2, based on a study conducted at two localities in the centre by Fauna & Flora International (FFI) and Biodiversity and Nature Conservation Association (BANCA) in 2009 (Geissmann et al., 2013). The low gibbon density in this area is due to hunting pressure, habitat loss and genetic isolation from logging and agricultural activities (Geissmann et al., 2013). Overall, 14% of both strongholds face a high threat level, 55% face a medium level of threat and 31% show a low threat level. Only 5% of stronghold 4% and 7% of stronghold 5 are within protected areas. In China, the gibbon populations outside protected areas are threatened by poaching and habitat loss.

7. Sites outside the suitable patches

A total of 46 out of the 90 sites fall outside suitable patches and, therefore, are excluded from the strongholds. Because they are found in small fragments of suitable habitat, the resident populations are at high extinction risk in the short term. The 46 sites are grouped into 18 highlighted areas (Fig. 4c).

In the western hoolock range, a total of 37 sites grouped into nine highlighted areas (1, 2, 3, 4, 5, 6, 14, 15 and 17) are found outside suitable patches and suitable habitat. Four highlighted areas (1, 2, 3 and 5) are entirely located in India, three (6, 15 and 17) are located in Myanmar, whereas two (4, 14) are transborder areas between India and Bangladesh and between Bangladesh and Myanmar, respectively.

In India, highlighted area 1 consists of 11 sites with an estimated 40 population groups (Kakati et al., 2009), mostly found outside suitable habitat. Gibbons populations in forest fragments degraded by past and recent logging events are likely to disappear soon if threats persist (Kakati et al., 2009). Sites in highlighted areas 2 and 3 also face a high threat level owing to scattered forest fragments. Choudhury (2006) reported a density estimate of 1.47 individuals/km^2 (0.44 groups/km^2) at these sites, linked to the threats of habitat fragmentation and poaching.

One site in highlighted area 4, in India, shows a medium threat level. A survey from 2012 shows an estimated population of 7 groups, due to hunting and fragmentation pressure (Deb et al., 2014). Despite being too small to be considered a stronghold, highlighted area 5 falls entirely inside a protected area and has an estimated population of 50 individuals, based on a survey conducted in 2001 (Choudhury, 2006). The forest in the area appears to have significantly degraded within the last 17 years between 2001 and 2018.

In Bangladesh, two transboundary highlighted areas were found, namely areas 4 and 14, which respectively span the borders with India and Myanmar. Surveys between 1997 and 2002 by Islam et al. (2006) recorded 24 groups at seven sites in highlighted area 4 and 60 groups in highlighted area 14 while identifying small population sizes and habitat fragmentation as major threats to the survival of hoolock gibbons. Highlighted areas 6, 15 and 17 in Myanmar show a low threat level overall. Although the presence of gibbons in highlighted area 6 was last recorded in 1916 (Jenkins, 1990), the likelihood of the species survival is high due to its low threat level and location within the suitable habitat. Some sites in highlighted area 15 fall within protected areas with a density estimate of 0.32 groups/km^2 in small forest blocks. Highlighted area 16 is in the fragmented forest area caused by shifting cultivation (Geissmann et al., 2013). One site in highlighted area 14 in Myanmar falls outside the suitable habitat with a low level of threat.

In the eastern hoolock range, a total of eight highlighted areas were recorded (7, 8, 9, 10, 11, 13, 16 and 18), and all of them are located in Myanmar.

Two highlighted areas (number 9 and 16) fall within protected areas. However, the species absence was confirmed in number 16, located in Panlaung-pyadalin Cave Wildlife Sanctuary (Oikos and BANCA, 2011). For highlighted area 9, located in the Indawgyi Wildlife Sanctuary with a low level of threat, a recent extensive survey shows a very high gibbon density estimate of 4.64 groups/km^2 (Lwin et al., 2021). Highlighted areas 7, 8, 11, 13 and 18 are within the suitable habitat, while area 10 falls within the marginal habitat. Highlighted area 18 shows a high threat level, areas 10 and 11 face medium threat levels, whereas areas 7, 8 and 13 exhibit low threat levels.

The Gaoligong hoolock range showed only one highlighted area (12) where the species was recorded in 2000 during the national tiger survey in Myanmar (Lynam, 2003). Despite being too small to be included in a stronghold, the suitable habitat shows a low threat level, making it likely to find existing populations within.

8. Conservation implications

The most urgent need for the western hoolock gibbon conservation is managing the Bangladesh remnant population found both in strongholds and in smaller fragments because gibbon habitat all over Bangladesh have been destroyed at an alarming rate within the last decade (Hansan and Feeroz, 2011). Priority conservation actions should focus on designating new protected areas at strongholds number 21 and over the Bangladesh portion of transboundary stronghold number 23; transboundary conservation between Bangladesh and Myanmar should be initiated. To save scattered populations in highlighted areas, translocation of species to nearby strongholds should be considered.

In Myanmar, conservation of the western hoolock in stronghold 24 should consider expanding the protection and providing technical and financial support to existing protected areas for effective management.

For the populations in transboundary strongholds 2, 12, 16 and 22, there is a need for collaboration between India and Myanmar to conserve the species. It could be assumed that the protected area is sufficient to support the remaining populations of the eastern hoolock as the area faces a low level of threat both in India and Myanmar. Accordingly, effective management practices such as law enforcement should be maintained in the protected areas in India and Myanmar for the long-term survival of the populations. Regarding the Expected Presence strongholds in Myanmar, an immediate survey is recommended to confirm the species presence and estimate their population sizes. Given the limited knowledge of the status of Gaoligong hoolock in stronghold number 4 in Myanmar, population surveys are of utmost importance going forward. Consequently, joint conservation action plans should be developed by China and Myanmar for the long-term survival of this species.

In conclusion, we recommend the implementation of the following actions for preserving present hoolock gibbon populations and preventing local extinction: 1) initiate transboundary conservation programmes between China and Myanmar for Gaoligong hoolock, between Myanmar and India and Myanmar and Bangladesh for the western hoolock to establish gibbon protected areas, 2) establish population monitoring and conservation awareness programmes at strongholds with a high level of threat and highlighted areas, 3) consider a translocation programme for scattered populations, particularly in Bangladesh, 4) confirm species absence/ presence and study populations in Expected Presence strongholds.

Ethical standards

The submitted research comply with the journal’s Code of Conduct for authors contributing articles. This research did not involve human subjects, experimentation with animals and/or collection of specimens.

CRediT authorship contribution statement

All authors designed the project and contributed equally in analyzing the data and writing the manuscript.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ngwe Lwin reports financial support was provided by Petchra PrajomKlao Scholarship Program for PhD.

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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.e01726.

Appendix

(see Table A1).

Table A1
The model set shown relationship of variables ranking based on the lowest Akaike's Information Criterion (AIC) value LTGtr=Lowland tropical grassland, HDHtr=Highly degraded habitat, LDHtr=Less disturbance habitat, EVtr=Evergreen forest, MDFtr=MDF with DDF (HKK type), MDFDtr=MDF dry (BagoYoma type), PINEtr=PINE, MDFFtr=MDF with Fagaceae, HStr=Herb and shrub, DStr=Dry shrub (central dry zone), MGtr=Montane grassland (Tibet type), alt=Elevation, SLOtr=Slope.

Rank	Model	Log-likelihood	K	AICc	Delta_AICc	AICcWt	Cum.Wt
1	alt+HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+DStr+MGtr	-5712.92	10	11446	0	0.31	0.31
2	alt+HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+DStr	-5714.17	9	11446	0.49	0.24	0.55
3	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+DStr	-5714.1	10	11448	2.36	0.09	0.88
4	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+MDFFtr+DStr+MGtr	-5712.47	12	11449	3.1	0.07	0.95
5	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+MDFFtr+DStr	-5713.72	11	11449	3.6	0.05	1
6	alt+HDHtr+LDHtr+EVtr+MDFtr+PINEtr+DStr	-5720.71	8	11457	11.57	0	1
7	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+PINEtr+DStr	-5720.43	9	11459	13	0	1
8	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+PINEtr+MDFFtr+DStr	-5719.98	10	11460	14.11	0	1
9	HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+DStr	-5724	8	11464	18.16	0	1
10	HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+DStr	-5724	8	11464	18.16	0	1
11	HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+PINEtr+MDFFtr+DStr+MGtr	-5722.86	10	11466	19.88	0	1
12	alt+SLOtr+LDHtr+EVtr+MDFtr+PINEtr+DStr	-5728.74	8	11473	27.62	0	1
13	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+DStr	-5732.03	9	11482	36.21	0	1
14	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+MDFFtr+DStr	-5731.55	10	11483	37.26	0	1
15	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr+DStr	-5736.6	8	11489	43.34	0	1
16	alt+SLOtr+HDHtr+LDHtr+EVtr+PINEtr+DStr	-5738.5	8	11493	47.16	0	1
17	alt+SLOtr+HDHtr+LDHtr+EVtr+MDFtr	-5749.01	7	11512	66.18	0	1
18	alt+SLOtr+HDHtr+LDHtr+EVtr+DStr	-5753.13	7	11520	74.41	0	1
19	alt+SLOtr+HDHtr+LDHtr+EVtr+DStr	-5753.13	7	11520	74.41	0	1
20	alt+LDHtr+EVtr+MDFtr	-5755.99	5	11522	76.13	0	1
21	EVtr+alt+LDHtr+DStr	-5757.2	5	11524	78.55	0	1
22	EVtr+alt+SLOtr+LDHtr+DStr	-5756.53	6	11525	79.21	0	1
23	HDHtr+LDHtr+EVtr+MDFtr+MDFDtr+DStr	-5759.53	7	11533	87.2	0	1
24	alt+SLOtr+LDHtr+EVtr	-5762.03	5	11534	88.2	0	1
25	alt+SLOtr+EVtr	-5773.68	4	11555	109.5	0	1
26	alt+EVtr	-5774.92	3	11556	109.99	0	1
27	EVtr+LDHtr+DStr	-5777	4	11562	116.14	0	1
28	EVtr	-5787.52	2	11579	133.18	0	1
29	PINEtr	-5788.83	2	11582	135.8	0	1
30	LDHtr	-5791	2	11586	140.14	0	1
31	MDFtr	-5792.39	2	11589	142.93	0	1
32	Alt	-5801.61	2	11607	161.37	0	1
33	HDHtr	-5802.96	2	11610	164.07	0	1
34	DStr	-5803.23	2	11610	164.6	0	1
35	MDFDtr	-5804.84	2	11614	167.82	0	1
36	SLOtr	-5805.3	2	11615	168.74	0	1
37	MGtr	-5807.8	2	11620	173.74	0	1
38	MDFFtr	-5808.48	2	11621	175.1	0	1
39	LTGtr	-5809.19	2	11622	176.52	0	1
40	HStr	-5809.28	2	11623	176.71	0	1

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