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Population viability reveals hidden extinction risk within stable habitat in fragmenting mountain landscapes: A case study from the skywalker gibbon

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ABSTRACT

Stable habitat patches are areas that remain suitable across decades of landscape change. They can guide conservation in fragmenting landscapes, but their capacity to sustain viable populations remains poorly quantified. Using records from the 1980s to the 2020s, we reconstructed habitat trajectories for the endangered skywalker gibbon (*Hoolock tianxing*) in Mt. Gaoligong, southwest China. We combined ensemble ecological niche models with population viability analysis under continuous-habitat and road-isolation scenarios. Suitable habitat declined by 26%, with losses concentrated below 2000 m, especially at 1600–2000 m (34%). Habitat below 1600 m partially recovered after 2000 but remained below the 1980s baseline. Four stable patches were identified; three support the known Chinese population. Carrying capacities reached 28 times current population sizes, suggesting patch size alone does not limit recovery. Population viability analysis showed that road isolation, slow life history, and human pressures create hidden extinction risks within stable patches. Longer breeding intervals increased risk to 12%; high hunting pressure raised it to 66%. With road isolation, risk reached 100% under high hunting pressure. We recommend zero-poaching enforcement, low-elevation restoration, canopy bridges, translocation, and protected-area expansion. Our workflow offers a transferable conservation prioritization framework in mountain fragmenting landscapes.

Keywords: Extinction debt; Mountain conservation; Road isolation; Skywalker gibbon; Population viability

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INTRODUCTION

Human pressures have caused continuous habitat changes, including contraction and fragmentation (Yang et al., 2023a). Hunting and other anthropogenic threats further accelerate population decline (Benítez-López et al., 2017; Ralimanana et al., 2022). These threats do not act in isolation, nor are they static. In particular, habitat fragmentation is a continuous temporal process rather than a static spatial pattern (Fletcher et al., 2026). This process interacts with hunting and other pressures, but animal populations respond slowly. For long-lived species, ecological time lags can generate extinction debt, which refers to delayed future extinction caused by past habitat loss or fragmentation even when populations persist for decades after disturbance (Watts et al., 2020). Static landscape snapshots that compare current configurations and assume equilibrium may therefore severely misjudge population fate (Fletcher et al., 2026). Preventing such misjudgments requires an explicit understanding of historical baselines and landscape trajectories. This need is especially pressing for mountain biodiversity conservation. In mountain ecosystems, human activities and land use change concentrate in productive low elevation zones. As low elevation habitat disappears, mountain species may be forced to retreat upward into higher elevations. The loss of these lower elevation corridors disconnects remnant populations across the landscape, accelerating the fragmentation process. Understanding how this elevational pattern of habitat loss shapes population viability is therefore critical for mountain species conservation.

Stable habitat patches refer to areas that were consistently predicted as suitable habitat across multiple historical periods, which may function as refugia under environmental stress and

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potential sources for recovery when threats decline (Chapman et al., 2018; Selwood & Zimmer, 2020). In mountain landscapes, such patches often represent persistent high elevation refugia that survive while surrounding low elevation habitats are progressively degraded (Yang et al., 2023b). Empirical evidence demonstrates that such stable patches sustain the long-term persistence of diverse taxa, including montane small mammals in Romania (Benedek et al., 2022), primates in Kibale (Lwanga et al., 2011), and the western black crested gibbon (*Nomascus concolor* Harlan, 1826) in China (Yang et al., 2023b). However, populations may face extinction due to small population size and other threats even within stable patches (Barreto et al., 2022), particularly when continuing fragmentation creates isolation that pushes populations into extinction debt (Fletcher et al., 2026).

Population Viability Analysis (PVA) provides a quantitative framework to assess extinction risk by integrating demographic, genetic, and environmental factors, and has been used to inform conservation strategies for many threatened species, such as the grey wolves (*Canis lupus* Linnaeus, 1758) (Hatlauf et al., 2024), Père David's deer (*Elaphurus davidianus* Milne-Edwards, 1866) (Li et al., 2023), and Cao-vit gibbon (*Nomascus nasutus* Kunkel d'Herculais, 1884) (Fan et al., 2013b). However, most studies have not incorporated habitat dynamics into population viability assessments (Lacy, 2019), because the prevailing space-for-time paradigm treats fragmentation as a static pattern rather than a temporal process (Fletcher et al., 2026). Yet few studies have jointly evaluated multi-decadal habitat trajectories with demographic responses (Andersen et al., 2017; Barreto et al., 2022). Consequently, we lack a framework that links long-term habitat dynamics to time-lagged population viability. This gap is especially consequential for mountain species, whose habitats contract upward over time in patterns invisible to static analyses.

The skywalker hoolock gibbon (*Hoolock tianxing*; hereafter skywalker gibbon), also known as the Gaoligong hoolock gibbon, is the most recently diverged species within the family Hylobatidae, and was described in science in 2017 (Fan et al., 2017; Wang et al., 2026). The species is currently listed as Endangered on the IUCN Red List and was recognized as one of the world's 25 most endangered primates in 2018–2019 (Schwitzer et al., 2019) and 2022–2023 (Mittermeier et al., 2022). In China, it is listed as a Class I protected animal and critically endangered species requiring urgent conservation measures. Historically, the skywalker gibbon was widely distributed in the west bank of the Salween River (the Nujiang River in Chinese) (Ma & Wang 1988). However, poaching, commercial logging, and agricultural expansion have drastically reduced its historical range (Fan, 2017). By 2017, the species was estimated to have a small population of less than 150 individuals consisting of 32–34 groups and 11 solitary individuals, with most patches supporting no more than four groups (Zhang et al., 2020). Approximately 50% of the population was located outside nature reserves, suffering habitat degradation and fragmentation caused by human disturbances and road construction (Zhang et al., 2020). Although strict gun control has substantially reduced poaching on the Chinese side, expanding road networks increasingly isolate gibbon groups and compound the connectivity loss caused by low-elevation habitat degradation (Yang et al., 2023b; Zhu et al., 2025). Beyond its conservation urgency, the skywalker gibbon offers an unusual methodological opportunity: integrating historical and contemporary data yields one of the few cross-generational habitat-demography datasets available for endangered mammals.

To address this gap, we reconstructed habitat trajectories from the 1980s to the 2020s, identified stable habitat patches, and used PVA to test how road-induced fragmentation altered population viability by comparing a continuous-habitat scenario with a road-isolation scenario applied to the Yingjiang-Tengchong region, where road networks are expanding outside protected areas. Our results provide targeted management recommendations for the skywalker gibbon's long-term survival in China and offer a transferable workflow for other endangered species in fragmented mountain landscapes.

MATERIALS AND METHODS

Data collection

We followed the standardized protocols described by (Yang et al., 2018) to integrate historical occurrence records of the skywalker hoolock gibbon (*H. tianxing*) from the 1980s and 2000s. A comprehensive list of historical survey sources and justifications for data integration across different periods are provided in the Supplementary Material. Data were synthesized from previous literature, museum specimens, local chronicles, and archival records, resulting in 113 records for the 1980s and 81 records for the 2000s.

Between 2018 and 2025, we conducted field surveys across Mt. Gaoligong and the Yingjiang–Tengchong region, covering>50% of the species' known historical range in China (Zhang et al., 2020). Survey teams performed acoustic monitoring from ridge-top listening posts from dawn until noon for at least six consecutive days per site. We utilized triangulation to determine coordinates of singing groups, distinguishing distinct groups and solitary individuals by singing time, location, and vocal composition (Brockelman & Srikosamatara, 1993; Fan et al., 2022). Solitary status was further confirmed via direct observation in fragmented forest patches.

From 2023 to 2025, we applied 226 Autonomous Recording Units in remote or inaccessible terrain (Guo et al., 2024; Wang et al., 2024). The devices recorded daily from 0600h to 1500h, totaling 61 333 hours of audio. Gibbon vocalizations were extracted using a custom algorithm (Guo et al., 2024; Wang et al., 2024) and validated by singing type, location, and time. These efforts confirmed 82% of gibbon groups recorded after 2020; combined with field surveys, they yielded 61 contemporary records.

We reconstructed multi-decadal trajectories by synthesizing museum specimens, local chronicles, and modern field surveys (2018–2025) with acoustic monitoring (2023–2025). This multi-source approach yielded occurrence records spanning the 1980s to the 2020s that no single methodology could provide independently.

To minimize spatial autocorrelation, we applied a spatial thinning technique using a 0.5 km radius, which corresponds to the species' average home range of approximately 100 ha (Fei et al., 2022; Zhang et al., 2014), utilizing the spThin package in R (Aiello-Lammens et al., 2015; Yang et al., 2023b). The final dataset for modeling comprised 107 records for the 1980s, 75 for the 2000s, and 56 for the 2020s.

Environmental variables

We obtained climate data (monthly temperature and

precipitation) from ClimateAP v.3.20 (https://web.climateap.net/) (Wang et al., 2017). To account for the time-lagged effect of climate on habitat suitability and ensure temporal correspondence with our occurrence data, we selected three 30-year climatological periods that characterize the long-term environmental conditions preceding each survey period: 1951–1980 (representing the baseline climate for the 1980s), 1971–2000 (for the 2000s), and 1991–2020 (for the 2020s) (Carscadden et al., 2020). The 30-year period is widely used in climatological studies because it provides a statistically robust basis for calculating long-term averages (Fick & Hijmans, 2017; Harris et al., 2020; Navarro-Racines et al., 2020). Digital elevation data (100 m resolution) was acquired from 91 weitu (www.91weitu.com). Nineteen bioclimatic variables were generated using the dismo package in R (Navarro-Racines et al., 2020). To represent different decades, we selected the following representative years: 1985 for the 1980s, 2000 for the 2000s, and 2020 for the 2020s. All raster layers were standardized to a 100 m resolution.

Forest quality modeling

We compiled 356 high-quality forest occurrence records between 2015 and 2025 based on field surveys (Supplementary Figure S2). We defined high-quality forests by three criteria: the presence of food trees, the absence of large-scale logging in recent decades, and historical records of gibbon distribution within the last 30 years. These points were obtained for modeling. To reduce spatial autocorrelation, a 0.5 km thinning radius was applied using the spThin R package (Aiello-Lammens et al., 2015; Yang et al., 2023b), resulting in 171 independent points.

Land cover data were derived from the GLC_FCS30D dataset (Liu et al., 2025). Based on our field observations and published descriptions of forest use by Chinese gibbons (Fan, 2017; Ni et al., 2014), we treated evergreen and deciduous broadleaf forest as primary habitat and retained evergreen coniferous and mixed forest as potential movement habitat. We combined these classes to construct a binary forest mask (1=forest, 0=non-forest). To derive a proxy for human disturbance, we calculated the Euclidean distance from each grid cell to the nearest forest patch for each of the three study periods using the terra package. These distance values were normalized to a range of 0 to 1, where 0 represents the closest proximity and 1 the farthest, under the assumption that disturbance intensity increases with distance from forest cover. We also generated 2000 pseudo-absence points per period, spatially weighted by the normalized disturbance layer, using the dismo package (Hijmans et al., 2021). The final set of predictor variables included Mean Annual Temperature (Bio1), Annual Precipitation (Bio12), distance to forest patch, and elevation.

Based on these inputs, we applied an ensemble ecological niche modeling (ENM) framework using the biomod2 package in R. Following (Yang et al., 2023a), we integrated seven algorithms: Generalized Boosting Model (GBM), Multiple Adaptive Regression Splines (MARS), Generalized Additive Model (GAM), Random Forest (RF), Random Forest downsampled (RFd), eXtreme Gradient Boosting Training (XGBoost), and Maximum Entropy (MAXNET). The resulting forest quality map (scaled 0–1000) was then used as a key input variable for the subsequent species distribution modeling. Further methodological details were provided in the Supplementary Material.

Gibbon potential suitable habitat modeling

To control for sampling bias, we employed a dual-strategy approach to generate 2000 pseudo-absence points per period. First, 1000 pseudo-absences were generated using distance-weighted sampling based on known occurrence records. Second, acknowledging strong dependence on forest by the skywalker gibbon (Fan, 2017; Zhang et al., 2020), an additional 1000 random points were generated specifically within non-forest areas.

We selected four key environmental variables for the gibbon distribution model, including Bio1, Bio12, Elevation, and the modelled forest quality (Table 1). These variables represent primate physiological demands for thermoregulation and food supply, as well as human impact (Chen et al., 2020; Fan et al., 2022; Kamilar & Beaudrot, 2018; Ni et al., 2015).

We then simulated the gibbon suitable habitat using the same ensemble framework (seven algorithms via biomod2) (Yang et al., 2023a). The resulting probability map (0–1) was converted into a binary presence-absence habitat map using a cut-off threshold derived from model evaluation scores. We then applied post-processing filters to exclude elevations above 2600 m and patches smaller than 100 ha based on the species' home-range requirement (Fan et al., 2022; Zhang et al., 2014). We also excluded areas east of the Nujiang River because this large river constitutes a major dispersal barrier for gibbons (Chatterjee, 2009). Finally, we calculated

Table 1 Variables for ecological niche modeling

Variable	Description	Source / Reference	Resolution / Unit
Mean annual temperature (Bio1)	Represents environment affecting gibbon physiology and vegetation growth	ClimateAP v.3.20 (Wang et al., 2017)	100 m (interpolation)
Annual precipitation (Bio12)	Reflects water availability influencing forest productivity and food supply	ClimateAP v.3.20 (Wang et al., 2017)	100 m (interpolation)
Elevation	Captures terrain complexity, human accessibility, and climatic gradients	91weitu DEM (100 m)	100 m
Forest distribution (binary forest / non-forest layer)	Identifies forest range; distinguishes forest from non-forest	GLC_FCS30D (Liu et al., 2025)	30 m (resampled to 100 m)
Forest quality index	Represents human disturbance and logging history; higher values=better quality forest	Field surveys+ecological niche modeling	100 m
Distance to forest patch	Euclidean distance to nearest intact forest patch, normalized 0–1; reflects accessibility and disturbance	Derived from Forest distribution	100 m
Distance to occurrence points	Normalized distance used as weights for pseudo-absence selection	Derived from occurrence database	100 m

the suitable habitat range size for the gibbon across three time periods: the 1980s, 2000s, and 2020s.

Identifying stable habitat patches

We defined stable habitat patches by overlaying potential habitat from the 1980s, 2000s, and 2020s (Yang et al., 2023b). Areas identified as potential suitable habitat across all three time periods were classified as "stable habitat patch", whereas areas identified in only one or two periods were classified as "temporary habitat patch". Stable habitat patches smaller than 100 ha were excluded as they cannot support a viable population (Fei et al., 2022; Zhang et al., 2014). To delineate an operational extent of potential dispersal, we applied a 10 km buffer around each detected group. This distance was informed by our field observations (Ren et al., 2018) and by evidence of long-distance connectivity in another gibbon species, the Hainan gibbon (*Nomascus hainanus*) (Hou et al., 2026). We merged overlapping buffers and used this extent to clip the habitat patches.

Following the clipping process, we estimated the environmental carrying capacity of the remaining habitat patches. We calculated the number of 500 m radius circles that could be accommodated within each patch boundary to represent the maximum number of groups (Fan et al., 2022). We then multiplied this count by an average group size of 3.6 individuals to determine the total environmental carrying capacity (K) (Zhang et al., 2020). This geometric method provides a spatial upper bound of carrying capacity. It does not account for food availability or other ecological constraints that reduce realized density. Consequently, we excluded patches unable to accommodate a single gibbon group (less than one 500 m radius circle) because these areas likely cannot support population persistence due to geometric constraints.

We created a 500 m buffer around each gibbon occurrence record from the 2020s. A gibbon group was considered to inhabit a stable patch if its record buffer overlapped with any portion of that stable patch (Yang et al., 2023b). We also assessed the range of protected area (PA) in Yunnan Province in China to estimate the PA coverage.

Population viability analysis (PVA)

We conducted a PVA using Vortex v.10.8.1 to project population trends over 50 years with 1 000 iterations. Extinction was defined as the point where only one sex remained (Fan & Jiang, 2007; Turvey et al., 2024). Carrying capacity (K) for each stable patch was incorporated into the model based on the geometric estimates described above. Patches or sub-patches containing only a single individual or single-sex groups were considered functionally extinct and were therefore excluded from the PVA. We selected a long-term monogamous system with inbreeding depression (lethal equivalents=6) (Lacy, 2019).

All demographic inputs were synthesized from published literature and our 15-year long-term field monitoring (since 2009). These parameters were cross-validated by the field survey and acoustic monitoring records described in the data collection section, ensuring the baseline model was grounded in empirical evidence (Table 2). To ensure demographic equilibrium, we initialized the population using a stable age distribution derived from the life table (Akçakaya & Sjögren-Gulve, 2000; Lacy, 2019).

In the baseline scenario, females and males first reproduce at ages 10 and 12, respectively (Fan & Jiang, 2007), with a 3-year breeding interval (Zhong et al., 2025). Age-specific mortality was characterized by 20% juvenile mortality, while adult mortality remained low (0%–5%) based on longitudinal monitoring (Fan & Jiang, 2007; Fan et al., 2013b; Turvey et al., 2024) (detail in Supplementary Table S1). Notably, the baseline assumes zero hunting pressure to reflect the contemporary conservation reality in China, where strict gun bans and natural forest protection programs have effectively eliminated poaching in the study regions over the past decade. We also incorporated low-frequency catastrophic events (1% annual probability; negligible demographic impact, see Supplementary Material).

We performed sensitivity analysis to evaluate the influence of reproductive age, breeding interval, and hunting pressure on population persistence. Specifically, we tested scenarios with varying hunting frequencies (removal of one adult pair every 2, 5, or 10 years) and extended breeding intervals (4–5 years) to assess population thresholds under potential threats (Table 3). Each setting was replicated ten times. To identify the parameters with the strongest influence on population viability, we compared the extinction probability and the average percentage population decline relative to the baseline

Table 2 Sources for Population Viability Analysis (PVA) parameters

Parameter	Baseline Value	Source
Mating System	Monogamy	Confirmed via 15-year field monitoring (since 2009) and standardized survey protocols for family groups (Zhang et al., 2020).
Reproductive Age	Female: 10 years; Male: 12 years	Derived from life-history monitoring in Mt. Gaoligong, Yingjiang; also from previous research data of gibbon species (Fan & Jiang, 2007; Fan et al., 2013b)
Breeding Interval	3 years (Range: 3–6)	Based on 5 focal groups (Zhong et al., 2025); sensitivity scenarios (4–6) account for seasonal fruit shortages.
Reproductive Success	81.8% (SD: 18.2%)	Derived from 18.2% environmental variance in breeding success to reflect environmental fluctuations (Fan et al., 2013b).
Age-Specific Mortality	Supplementary Table S1	High juvenile mortality (20%) decreasing with age, based on field surveys and established primate life tables (Fan & Jiang, 2007; Fan et al., 2013b; Turvey et al., 2024).
Male Breeding Pool	100%	Reflects full mate monopolization observed in monogamous gibbon social structures.
Lethal Equivalents	6	Conservative standard for small population inbreeding depression (Lacy, 2019).
Catastrophes	1% probability	Based on low-frequency landslide and fire records in Mt. Gaoligong (99% survival probability).
Carrying Capacity (K)	Patch-specific	Calculated via geometric group density (500 m radius) and forest quality modeling (Supplementary Table S4).

Table 3 Parameter settings for sensitivity analysis

Category	Settings	Parameters
Baseline		Females: 10 years; Males: 12 years; 33% adult females breed; Interval: 3 years; No hunting
Reproduction Age	Early	Females: 8 years; Males: 10 years
	Delay	Females: 12 years; Males: 14 years
Breeding Interval	Moderate	25% adult females breed; Interval: 4 years
	Longer	20% adult females breed; Interval: 5 years
Hunting Pressure	High	Hunting every 2 years; one male+one female per event
	Moderate	Hunting every 5 years; one male+one female per event
	Low	Hunting every 10 years; one male+one female per event

across all settings.

Finally, we assessed the impact of fragmentation specifically in the Yingjiang-Tengchong region, where expanding road networks pose increasing isolation threat. This contrasts with the Gaoligongshan Nature Reserve, where gibbon habitat remains relatively connected. We downloaded road network data from 91 Weitu and OpenStreetMap and subsequently verified these vectors using satellite imagery and field survey records. We operationally classified roads as potential functional dispersal barriers when they were at least 6 m wide and lacked canopy connectivity. This criterion was based on field observations in our study area, where no gibbon crossings were recorded across such roads, and was broadly consistent with previous observations of the siamang (*Symphalangus syndactylus*) (Fleagle, 1976). We applied this criterion to satellite imagery from 91 weitu and further checked road width and canopy discontinuity using field survey records. The identified roads were then used to geometrically split stable habitat patches into isolated sub-patches. We then designed two scenarios. The continuous-habitat scenario treats stable habitat patches as continuous units. In contrast, the road-isolation scenario fragments these patches based on the identified barriers. Under the second scenario, we classified any resulting sub-patches smaller than the 100 ha home range requirement as unsuitable and excluded them from the analysis.

All PVA analyses were applied to two scenarios, including continuous-habitat and road-isolation scenarios.

RESULTS

Gibbon population

Over the past 40 years, gibbon occurrence records decreased from 113 to 61. Surveys conducted from 2020 to 2025 indicated that approximately 150 individuals remained in Yingjiang, Tengchong, and Mt. Gaoligong (Gaoligong National Nature Reserve) in China. Within Gaoligong National Nature Reserve, the population was further divided into two distinct subpopulations, located in the northwestern and southeastern areas. These findings align with those reported by Zhang et al. (2020).

Habitat dynamics across time periods

The mean True Skill Statistic (TSS) was 0.908 (SD=0.021), and the mean area under the ROC curve (AUC) was 0.989 (SD=0.004), indicating that the models were robust in identifying suitable habitat for gibbons. Forest quality had the highest variable importance, followed by elevation and climate variables (Supplementary Table S2).

Compared to the 1980s, potential suitable habitat declined by 17% in the 2000s and 26% in the 2020s (Figure 1A–C). Suitable habitat loss occurred across all elevation gradients. In areas below 1600 m, 76% of the suitable habitat was lost in the 2000s. However, the suitable habitat subsequently expanded, resulting in a loss of 23% of suitable habitat in the 2020s compared to the 1980s (Figure 1D). Suitable habitat between 1600 and 2000 m asl declined by 23% in the 2000s and 34% in the 2020s (Figure 1D).

The PA coverage of suitable habitat increased from 15% in the 1980s to 19% in the 2020s (Figure 1A–C). Despite this coverage increase, the range size of suitable habitat declined inside PAs by 14% in the 2000s and 7% in the 2020s. This loss was more severe outside PAs, reaching 17% in the 2000s and 29% in the 2020s. These results indicated that PAs mitigated habitat loss (Supplementary Table S3).

Stable habitat patches

Excluding road effects, we identified four stable habitat patches within the species' 10 km dispersal limit. These stable habitat patches were primarily located in two regions: Yingjiang-Tengchong along the China-Myanmar international border and the Mt. Gaoligong. Among these, Patch 1 (Yingjiang-Tengchong) was the largest (893 km^2) and located at the lowest average elevation (2040 m asl). In contrast, the patches in the Mt. Gaoligong occurred at higher elevations (2328 m and 2139 m asl). Patch sizes ranged from 33 km^2 (Patch 4, currently unoccupied) to 893 km^2 (Figure 2A).

Patch 1 and 2 were approximately 53 km apart, far exceeding the species' dispersal limit (Figure 2A). Within Mt. Gaoligong, Patches 2 and 4 are only 4 km apart but are functionally isolated by the mountain crest (>2600 m), while Patch 3 is approximately 42 km from both. Without feasible corridors, no natural exchange is possible between any patches.

Among these 4 patches, Patch 1 supported approximately 60% of all known individuals. Patch 4 was a historical gibbon habitat (it still had record in the 2000s, Supplementary Figure S1), but gibbons were locally extirpated recently from this area. According to home range size of skywalker gibbons, we estimated these 4 patches could theoretically sustain between 46 (Patch 4) and 2133 (Patch 1) individuals. This represents a potential population 6 (Patch 2)–28 (Patch 3) times higher than the current population (Figure 2; Supplementary Table S4). These values are theoretical maxima assuming uniform habitat quality; field based densities are substantially lower. In addition, the two gibbon-occupied patches (Patch 2 and 3) in Mt. Gaoligong had higher PA coverage (61%–62%). In contrast, the largest occupied patch in Yingjiang-Tengchong (Patch 1) had only 9% PA coverage (Figure 2A; Supplementary Table S4).

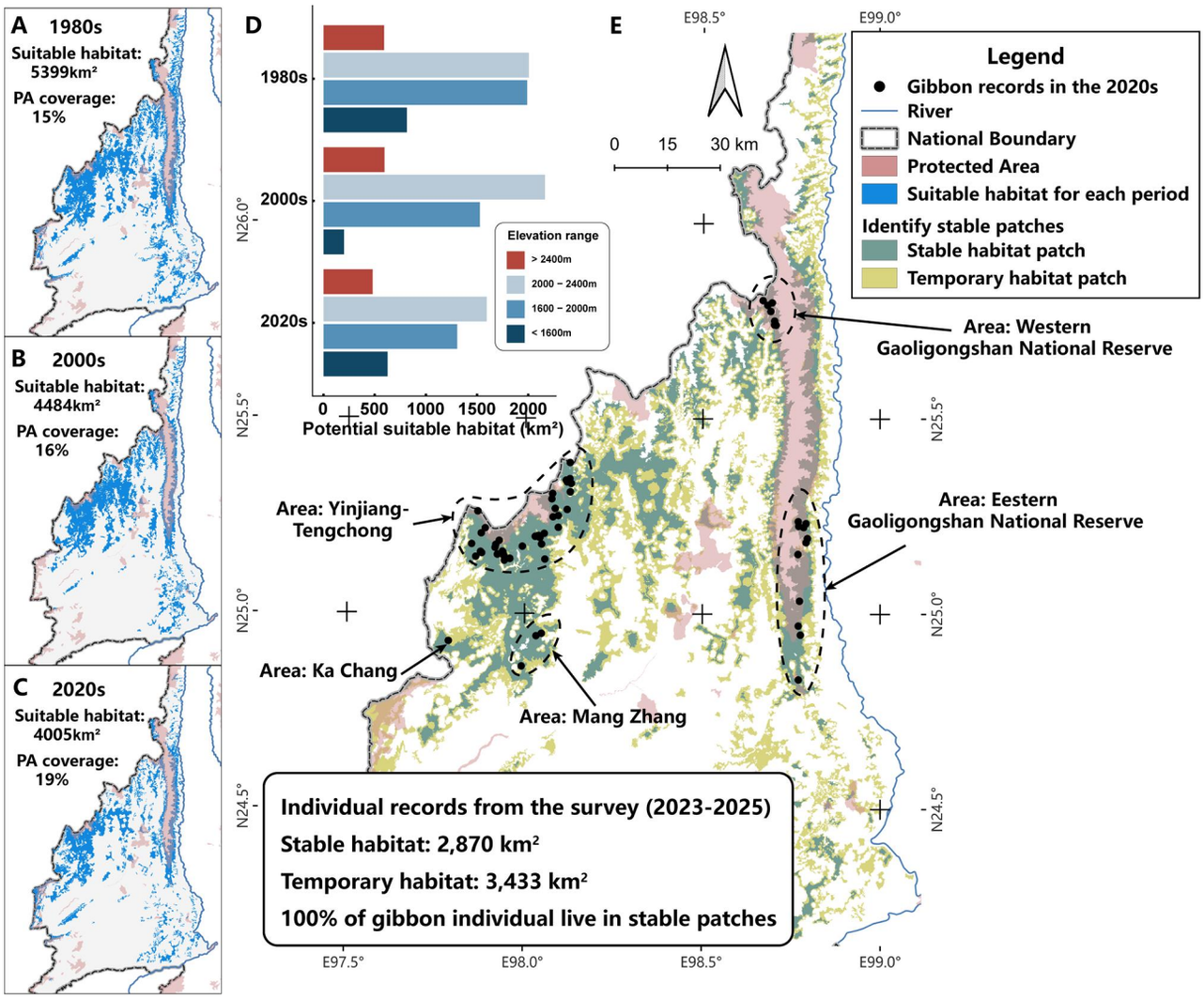


Figure 1 Potential suitable habitat changes and population distribution of the skywalker hoolock gibbon (1980s–2020s)

A–C: Potential suitable habitat changes and protected area coverage over time [1980s (1980–1990), 2000s (2000–2010), and 2020s (2020 until now)]. D: Suitable habitat across elevation classes. E: Stable versus temporary habitat patch overlaid with 2023–2025 survey records; all currently recorded individuals occurred within stable habitat patches.

We further considered road isolation in the Yingjiang-Tengchong region (originally Patch 1) because the population in Mt. Gaoligong is not currently threatened by road fragmentation. Under this scenario, the area was fragmented into 8 sub-patches, ranging in size from 18 to 164 km^2. Furthermore, sub-patches A to H were separated by road networks. Despite this isolation, these sub-patches could theoretically sustain between 46 (Patch H) and 351 (Patch G) gibbon individuals, representing a capacity 5.6 (Patch E) to 70.2 (Patch G) times higher than the current population (Figure 2B; Supplementary Table S4).

Population viability within stable patches

In the baseline situation without road isolation, all populations increased by 46% (SD: 2%) on average with no simulated extinctions within 50 years under the baseline assumptions. Earlier reproduction age nearly doubled population growth to 89%, whereas delaying it slowed growth to just 8%. In contrast, longer breeding intervals caused population declines of 36%–55% (Figure 3A) and introduced extinction risks of 5%–12% (Figure 3B). Hunting had the worst effect: while low pressure allowed marginal growth (12%), moderate and high pressures caused declines of 13% and 53%, respectively, with extinction risk arising at 66%. Patches 2 and 3 were particularly vulnerable, reaching 98% extinction risk under high hunting pressure (Figure 3B; Table 4; Supplementary Table S5).

If we considered road isolation in the Yingjiang-Tengchong border area, Patch 1 was divided into eight smaller patches. In the baseline simulation, the average population growth declined to just 6% (SD: 23%) (Figure 3C), and the risk of extinction rose to 27% on average (Figure 3D). Reproduction at an earlier age helped the population grow by 35%, but delayed reproduction caused the population to shrink by 8%. Longer breeding intervals caused the population to fall by 40%–55% and raised extinction risk to between 42% and 56%. Hunting had the worst effect of all: unlike the first scenario where low hunting was safe, here even low hunting pressure caused a 32% decline in population and a 55% risk of extinction. High hunting pressure was catastrophic, leading to a 91% population decline and a 100% simulated extinction risk (Figure 3C; Table 4; Supplementary Table S5).

Patch H was excluded as it contained only a single individual. With the exception of Patch A, all patches (B to G) faced extinction risks exceeding 50% under both low hunting pressure and increased breeding intervals (5 years). The

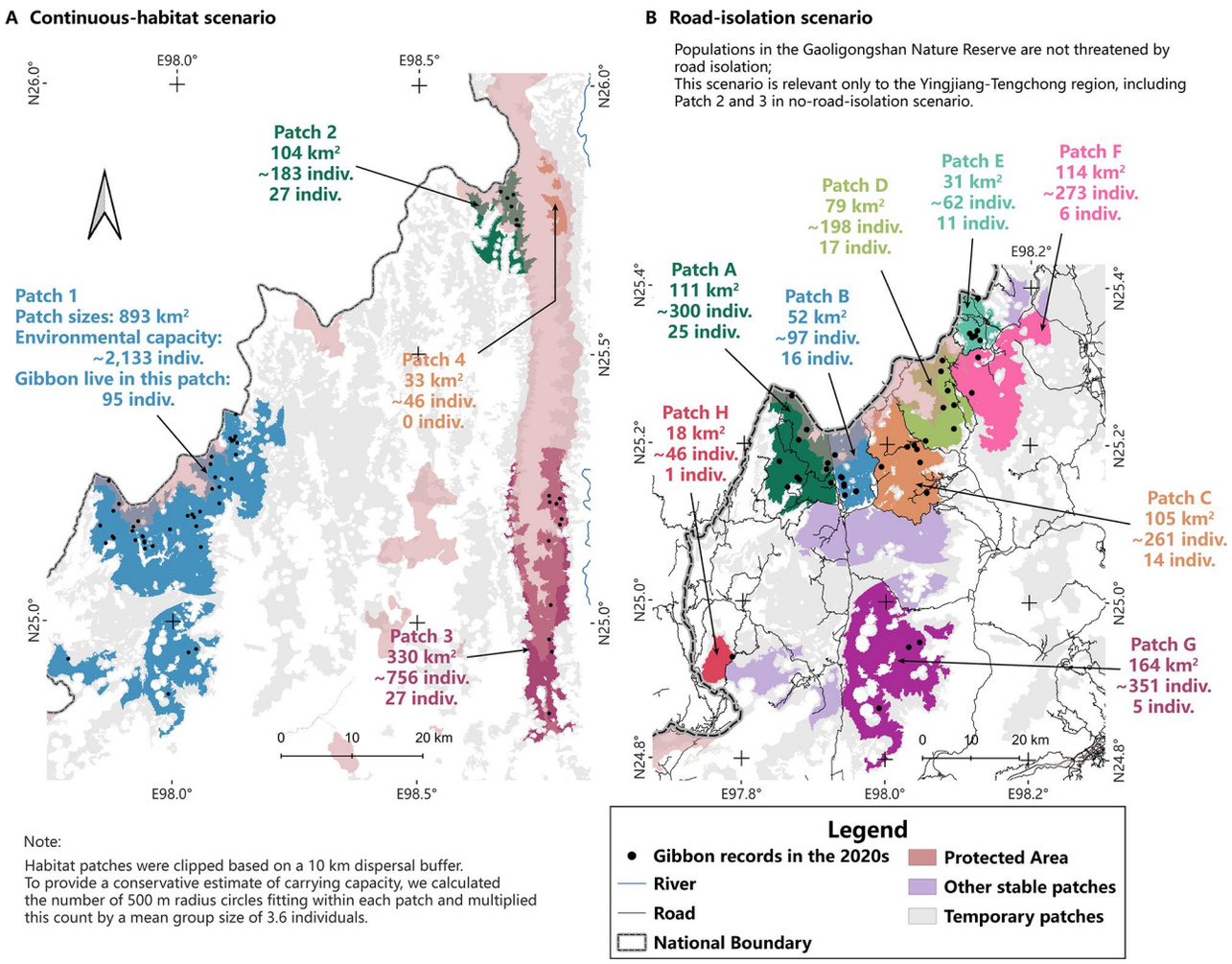


Figure 2 Comparison of stable patches for skywalker hoolock gibbon under continuous-habitat (A) and road-isolation (B) scenario

smallest patches, Patches F and G, faced inevitable extinction across all scenarios. Even under baseline conditions, they exhibited high extinction risks of 72% and 83%, respectively. While favorable factors reduced risks for larger patches, Patches F and G maintained risks above 66%, and any level of hunting pressure resulted in 100% extinction.

Patch 4 was excluded as it is currently unoccupied, and Patch H was excluded from PVA as it is considered functionally extinct with only a single individual (Figure 2).

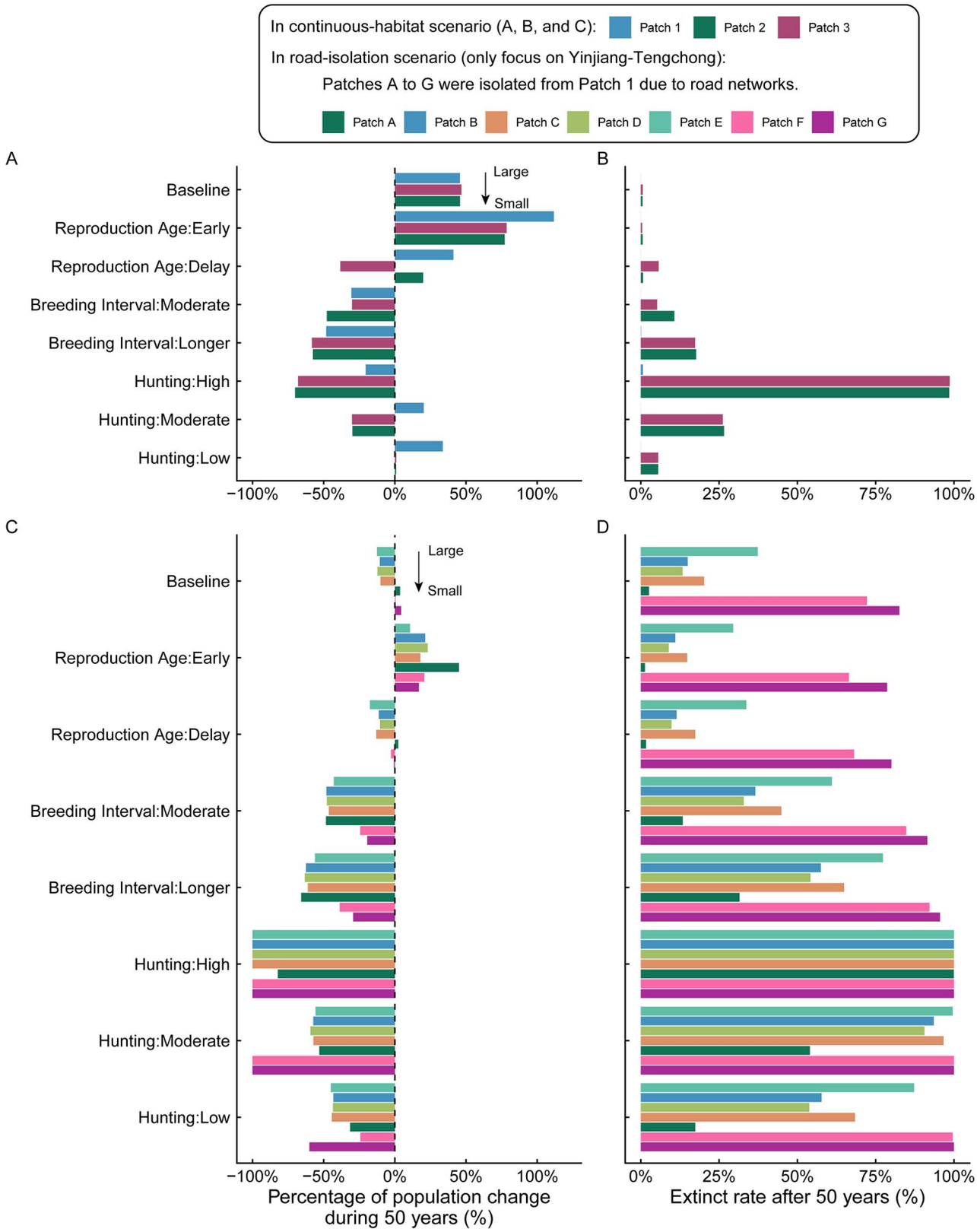
Panels (A–B) show population change and extinction risk under the continuous-habitat scenario. Panels (C–D) show the same metrics under the road-isolation scenario in the Yingjiang-Tengchong region. The y-axis represents variations in reproduction age, breeding interval, and hunting pressure relative to the baseline. Patch 4 was excluded as it is currently unoccupied, and Patch H was excluded from PVA as it is considered functionally extinct with only a single individual (Figure 2). Subpatches are shown from A to G to maintain correspondence with Figure 2.

DISCUSSION

We identified four stable habitat patches, three of which currently support the known Chinese population of the skywalker gibbon. Theoretically, these patches possess a carrying capacity up to 28 times greater than current numbers, suggesting that patch area within stable patches alone is unlikely to be the primary limitation to population recovery. However, PVA revealed that road isolation, extended breeding intervals, and hunting pressure are critical drivers of extinction risk.

Habitat change and population isolation

Over the past 30 years, habitat loss occurred across all elevations, yet the rate of loss has fluctuated. Specifically, after suffering severe losses in the 2000s, suitable habitat showed slight expansion by the 2020s in the low-elevation areas. These trends likely reflect shifting threats. Before 2000, commercial logging and hunting were likely the dominant threats to skywalker gibbons (State Forestry Administration, 1999). Similar threats led to local extinction of the northern white-cheeked gibbon (*Nomascus leucogenys* Ogilby, 1840) and white-handed gibbon (*Hylobates lar* Linnaeus, 1771) in Yunnan, China (Fan et al., 2014; Grueter et al., 2009). Since 2000, conservation policies such as gun bans and the Natural Forest Protection Project have facilitated habitat recovery, despite continuing small-scale disturbances (Fan et al., 2022). However, unlike western black crested gibbons (Fan et al., 2022), skywalker gibbons have not yet recolonized these recovered low-elevation forests. Continued cardamom cultivation, livestock grazing, and forest degradation may have limited habitat quality and connectivity, potentially contributing to the absence of recolonization in these areas (Fan, 2017; Yang et al., 2021; Zhang et al., 2020). This elevational pattern reflects a broader challenge for mountain biodiversity: although low-elevation habitat may recover in area, its



Note: Patch 4 was excluded as it is currently unoccupied, and Patch H was excluded from PVA as it is considered functionally extinct with only a single individual (Fig 2). Patch size from large to small

Figure 3 Sensitivity analysis of skywalker hoolock gibbon population viability to different factors

ecological quality and corridor function can remain impaired.

This mismatch between habitat recovery and population recolonization indicates a delayed population response to historical habitat change (Fletcher et al., 2026; Watts et al., 2020). The 26% habitat loss, particularly the 34% loss at 1 600 to 2000 m, displaced gibbon populations into high-elevation refuges and reduced connectivity among them. Although some low-elevation habitat has recovered since

Table 4 Population viability within stable patches under different scenarios

Scenario		Percentage of population change after 50 years (%) [mean±SD]	Extinction risk after 50 years (%) [mean±SD]
Continuous-habitat scenario:			
Baseline		+46% (2%)	0% (0%)
Reproduction Age	Early	+89% (16%)	0% (0%)
	Delay	+8% (34%)	2% (3%)
Breeding Interval	Moderate	–36% (8%)	5% (4%)
	Long	–55% (5%)	12% (8%)
Hunting	High	–53% (24%)	66% (47%)
	Moderate	–13% (24%)	18% (13%)
	Low	+12% (16%)	4% (3%)
Road-isolation scenario: Sub-patches A to G (fragmented from Patch 1) and Patches 2 & 3			
Baseline		+6% (23%)	27% (29%)
Reproduction Age	Early	+35% (25%)	24% (28%)
	Delay	–8% (15%)	25% (28%)
Breeding Interval	Moderate	–40% (11%)	42% (30%)
	Long	–55% (12%)	56% (28%)
Hunting	High	–91% (16%)	100% (1%)
	Moderate	–60% (24%)	76% (30%)
	Low	–32% (29%)	55% (36%)

2000, the absence of recolonization suggests that current population distribution still reflects this historical landscape configuration. This legacy is consistent with extinction debt and cannot be explained by a static snapshot of the 2020s landscape alone. Even if direct threats such as hunting and road disturbance are reduced, isolation among high-elevation habitat patches may continue to constrain population recovery unless connectivity is restored.

Population responses to different threats

Hunting has long been recognized as the most critical driver of gibbon population decline or extirpation in China (Fan, 2017; Jiang et al., 2006), and our PVA results confirmed that the skywalker gibbon remains extremely sensitive to hunting pressure. In the continuous-habitat scenario, Patches 2 and 3 are particularly susceptible, reaching a 98% extinction risk under high hunting pressure. The situation deteriorates further under road isolation, placing Patches G and F at critical risk. Compounding these threats, Patches A through F border Myanmar, where they face the additional threat of transboundary poaching. This vulnerability stems from the species' slow life history strategies, characterized by long lifespans and extended reproductive cycles. For such species, population persistence relies heavily on high adult survival rates; consequently, any anthropogenic disturbance that elevates adult mortality is often fatal. A similar pattern of vulnerability to adult loss has been observed in the silvery gibbon (*Hylobates moloch* Audebert, 1798) (Smith et al., 2018), pileated gibbon (*Hylobates pileatus* Gray, 1861) (Phoonjampa & Brockelman, 2008), the western black crested gibbon (Fan & Jiang, 2007), and other endangered species such as the lemurs (Brook et al., 2019). Given the high extinction risk of small populations, maintaining zero-poaching enforcement is the absolute prerequisite for long-term survival of skywalker gibbons in China. Furthermore, this underscores that habitat stability alone cannot ensure population persistence: extinction debt can accumulate invisibly even within high-capacity patches (Fletcher et al., 2026), and our PVA makes this debt explicit.

Breeding interval also strongly affects viability: extended intervals markedly increased extinction risk (Table 4). In fact, a 3-year breeding interval (baseline setting) may have overestimated the breeding output of the skywalker gibbon population in China. Gibbons are typical tropical dwellers, and prefer ripe fruits whenever they are available (Bartlett, 2011). However, the skywalker gibbons in China are found in high elevation montane forest, suffering fruit shortage during the cold winter seasons (Fan et al., 2013a). The annual diet of skywalker gibbons in the Mt. Gaoligong consisted of less than 40% fruits from <40 species (Fan et al., 2013a). Both the number of fruit species and the proportion of fruit in the diet are much lower than other gibbon populations living in low elevation habitats (Zhong et al., 2025). Monitoring of five groups in this area showed a breeding interval of 3–6 years (Hazitai et al., 2024). Increased energy intake by consuming more fruits may shorten the breeding interval of females (Zhong et al., 2025). Low elevation forest produced more fruits (Ma et al., 2026; Wang et al., 2025) and imposed lower thermoregulatory costs to animals (Dias et al., 2016; Fei et al., 2019; Zhong et al., 2025). However, fear of humans drives animals to avoid using the low elevation forest (Wang et al., 2025). By reducing human disturbances in low-elevation areas and increasing habituation, we can encourage gibbons to expand from their restricted high-elevation habitats into lower elevation areas, thereby shortening their breeding intervals, and consequently reducing the risk of extinction.

Our results indicate that high carrying capacity alone does not guarantee viability when road isolation restricts dispersal and mate exchange. Current gibbon numbers remain far below conservative carrying-capacity estimates. The skywalker gibbon's density (0.08–0.26 indiv./km^2) in China is low, even compared to other northern gibbon populations (*N. nasutus*: 4.5 indiv./km^2, (Fan et al., 2013b); *N. concolor* in Mt. Wuliang: 0.44 indiv./km^2 (Yang et al., 2023b). When road isolation was ignored, simulated extinction risk was negligible for all patches (Supplementary Table S5). However, isolation imposes a severe constraint on population viability in the Yingjiang-Tengchong region. Once we considered road

isolation in the simulations, extinction risk increased to 27% on average, and some small subpopulations were projected to face extremely high extinction risk. Because most of this area is outside any nature reserves, many paved roads were constructed to connect remote villages and alleviate poverty in these border areas. These roads created canopy gaps of 8–10 m, physically isolating groups; consistent with our previous findings from the Xiaopingan case, road isolation acts as a barrier to gibbon dispersal (Yang et al., 2023b). Additionally, these roads may facilitate human intrusion, compounding physical isolation with anthropogenic disturbance. Reduced dispersal may also limit mate acquisition and delay reproduction. Unlike hunting, which has been largely controlled in China, road networks continue to expand in this region, making road-induced isolation a persistent contemporary threat (Li et al., 2026). This threat is particularly important because roads in this mountainous landscape are concentrated in valley bottoms and low-elevation zones, where habitat loss has been most severe and the remaining corridors are critical for inter-group dispersal.

Methodological implications

Our study underscores that the apparent scarcity of long-term data in conservation partly reflects methodological reliance on single-source datasets. Conservation science has long treated the scarcity of multi-decadal baselines as a logistical failure that is an inevitable consequence of funding cycles shorter than organismal lifespans. We suggest this diagnosis is incomplete. The deeper limitation is methodological fragmentation: an implicit assumption that a single data source (e.g., museum archives, local chronicles, field surveys) must alone satisfy the temporal depth required for population viability inference. This assumption conflates data poverty with source poverty. In reality, many data-limited regions are source-rich but synthesis-poor: archives, chronicles, and field observations often coexist without ever being mobilized into a unified temporal scaffold. Recognizing this distinction is a prerequisite for diagnosing extinction debt across data-limited regions, where the data for long-term assessments may already exist, waiting only to be connected across sources and decades.

Conservation implications

Anti-poaching: Maintaining a zero-poaching baseline is essential for the population viability of the skywalker gibbon. Inside reserves, dedicated personnel assigned to focal groups translate anti-poaching goals into daily action. Outside protected areas, community-led models integrating traditional ecological knowledge are essential (Zhang et al., 2020). This approach is exemplified by the Lishu-Lamahe case, where women-led groups manage an “Ecological Public Affairs Fund” to mobilize villagers for habitat restoration and autonomous monitoring. Targeted conservation education in villages surrounding isolated patches may reduce opportunistic hunting risk (Emery Thompson et al., 2020).

Habitat restoration: The primary objective of habitat restoration is to recover low-altitude areas to facilitate the expansion of gibbon populations. First, active vegetation restoration is essential to enrich food availability. Initiatives such as the “Gibbon Cafeteria” (or “Gibbon Canteen”, https://www.cloudmountain.cn/) project launched by Cloud Mountain Conservation serve as a model, prioritizing the planting of native food species like *Gnetum montanum* and *Choerospondias axillaris*. Second, minimizing human disturbance is critical. Reducing anthropogenic pressure through nature education and community collaboration creates the necessary safety for gibbons to descend and inhabit these restored lowlands (Ma et al., 2026).

Canopy bridge: For road-caused fragmentation (e.g., between Patches A and F, Figure 2), artificial canopy bridges are an effective solution, having successfully reconnected habitats for 26 mammal species, including the Hainan gibbon (*N. hainanus*) (Chan et al., 2020; Gregory et al., 2017). These structures typically span 8–25 m to close canopy gaps and facilitate movement (Chan et al., 2020; Gregory et al., 2017). To date, we have installed 29 canopy bridges across the Yingjiang region (18 bridges in Lamahe village) and the Gaoligong region (11 bridges), with recent monitoring data confirming their success. While these results are promising, continuous monitoring of gibbon groups remains essential to identify precise movement corridors and determine optimal locations for future bridge construction.

Translocation program: Natural dispersal from patches in the Gaoligong Nature Reserve, Ka Chang, and Mang Zhang to their nearest neighbors is prevented by extreme distances (>17 km) or physical barriers such as the Mt. Gaoligong ridge (Figure 2). Because corridors are unfeasible in these areas, we recommend a translocation program to integrate isolated individuals into stable sub-populations.

PA expansion: Protected area expansion can remain the priority where feasible. Patch 1 holds about 60% of the skywalker gibbon population yet has only 9% PA coverage, making it an ideal candidate for PA expansion or national park designation. Where expansion is not possible, Other Effective Area-based Conservation Measures (OECMs) offer a practical alternative under Target 3 of the Kunming-Montreal Global Biodiversity Framework (2022). Lamahe already leads community-based monitoring and canopy bridge programs that deliver real conservation results, making it an ideal OECM case.

CONCLUSION

Our study shows that high-capacity stable patches can identify conservation priorities, but they do not necessarily guarantee demographic persistence for long-lived species in fragmenting landscapes. By integrating multi-decadal habitat trajectories with PVA, we show how extinction debt, slow life histories, and progressive habitat isolation create risks invisible to static landscape snapshots. Using the skywalker hoolock gibbon as a case study, we found that road isolation, hunting, and longer breeding intervals may drive even well-protected populations toward extinction. Conservation therefore needs to shift from passive protection to active interventions, specifically zero-poaching enforcement, low-elevation habitat restoration, canopy bridge construction and PA expansion. More broadly, this time-explicit, multi-source workflow demonstrates that multi-decadal viability is diagnosable without multi-decadal monolithic datasets. For mountain species facing habitat loss across elevation gradients, such time explicit frameworks are especially urgent. Low elevation habitat degradation concentrates populations into shrinking high elevation refuges while also severing the corridors that connect remaining populations. Without timely intervention that restores low elevation connectivity and halts the upward retreat of habitat, delayed action may leave no suitable habitat to protect.

SCIENTIFIC FIELD SURVEY PERMISSSION INFORMATION

Field surveys were conducted with permission from the Gaoligong National Nature Reserve and Yinjiang.

DATA AVAILABILITY

The data supporting this study are available in the Supporting Information accompanying this article. Any additional information required is available from the corresponding author upon reasonable request.

SUPPLEMENTARY DATA

Supplementary data provide the occurrence records, modelling procedures and demographic parameters used in this study, together with the complete scenario results (Supplementary Figures S1, S2; Supplementary Tables S1–S5). These materials support the findings in the main text.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

L.Y. and P.F.F. conceived and designed the study. L.Y., C.Y.Z., and H.L.F. conducted data collection. L.Y. performed the analyses and drafted the manuscript with C.Y.Z. and P.F.F. All authors revised the manuscript. All authors read and approved the final version of the manuscript.

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