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# A Piece of the Puzzle: Evaluating the Effectiveness of the Newly Designated Qilianshan National Park (China) and Its Contribution to Snow Leopard (*Panthera Uncia*) Habitat Connectivity

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## ABSTRACT

The assessment of landscape-level connectivity patterns is vital for wildlife conservation, particularly highly mobile carnivores such as the snow leopard (*Panthera uncia*), whose protection requires linking core populations beyond protected area boundaries. We evaluated the effectiveness of Qilianshan National Park (China), spanning Gansu and Qinghai provinces, in conserving key snow leopard habitats and dispersal routes. Using resistant kernel, graph-based, and factorial least-cost path analyses, we identified core habitat areas and major connecting corridors, comparing two resistance surfaces derived from habitat and genetic models. We ranked modeled core areas and corridors based on their contribution to overall connectivity and predicted snow leopard movement intensity. Results show that a substantial portion of core habitat patches and most modeled corridors are located outside the current park boundaries. The kernel analyses identified critical yet unprotected areas essential to range-wide connectivity. We identified core patches that form the backbone of the snow leopard habitat, as well as stepping-stone patches and corridors that maintain structural and functional landscape connectivity. Based on these findings, we give recommendations for the prioritization of certain management actions. While Qilianshan National Park safeguards some key snow leopard habitats, its current extent is insufficient to cover many critical areas and linkages. To support metapopulation persistence and gene flow across this pivotal region—potentially linking the Tibetan Plateau and southern Mongolia—conservation efforts for the Qilianshan National Park should prioritize the expansion of existing protections or the designation of new protected areas in strategic locations to conserve a greater number of core habitat areas and provide connectivity linkages among them.

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## Summary

- Evaluating habitat connectivity is important for the conservation management of wildlife species, especially wide-ranging carnivores like the snow leopard, which often venture beyond protected area boundaries.
- We investigated the effectiveness of Qilianshan National Park in China in providing protection for snow leopard habitat and routes for movement.
- By combining several modeling techniques and analyses, we produced a comprehensive picture of habitat quality and connectivity, and ranked areas and paths on their importance for supporting connectivity and snow leopard movement.
- Our results show that many high-quality habitats and key movement paths fall outside the current national park boundaries. We identify areas that are critical to overall connectivity and offer recommendations on where and how conservation actions should be prioritized.
- Expanding protection to include these areas could strengthen snow leopard habitat conservation and support healthy populations across a wider region.
- Conservation managers should consider enlarging the national park or designating new protected areas to safeguard more of the species' essential habitat.
- **Practitioner points**
  - Qilianshan National Park currently covers approximately 40% of core snow leopard habitat patches and 50% of key movement corridors between patches; expanding park boundaries to include additional high-value areas should be considered.
  - Qilianshan National Park sits at a pivotal biogeographic juncture between snow leopard populations in China and Mongolia and may serve as a climate refugium for the species.
  - Integrating multiple modeling methods in a comprehensive evaluation of habitat suitability and connectivity yields more robust and reliable results.

## 1 | Introduction

The home range requirements and dispersal abilities of apex predators are central considerations in their conservation and population management. These species often traverse vast areas, with their dispersal routes spanning a range of topographic, land cover, and land use conditions (Fattebert et al. 2013; Andersen et al. 2015; Janecka et al. 2017; Johansson et al. 2024). These routes may differ markedly from the specific habitat preferences associated with their home ranges (Palomares et al. 2000; Elliot et al. 2014; Johansson et al. 2016, 2024). Assessing the functional connectivity of such landscapes is therefore vital for understanding how environmental heterogeneity influences species dispersal (Tischendorf and Fahrig 2000; Saura and Torné 2009; Diniz et al. 2020). Landscapes that facilitate connectivity promote metapopulation stability and gene flow, thereby bolstering resilience to anthropogenic disturbances and climate change (Frankham 2005; Cushman et al. 2006; Baguette et al. 2013; Li et al. 2016; Hacker et al. 2023). Conversely, fragmentation can isolate populations, leading to

reduced genetic diversity and increased extinction risk (Gilpin and Soule 1986; Frankham 2005; Cushman et al. 2006).

Protected areas such as national parks are widely considered essential tools for habitat and population conservation. Conservation outcomes are more often successful within protected areas, where habitat quality, prey availability, predator protection, and protection from human disturbance are typically higher (Stoner et al. 2007; Gray et al. 2016; Van der Weyde et al. 2018; Wang et al. 2023). However, conservation planning must consider extending beyond park boundaries if it helps ensure functional connectivity within and around defined protected areas to support animal movement. A variety of synoptic connectivity modeling methods can be employed to guide this decision process. Resistant kernel analysis, for example, estimates expected movement density across landscapes and has been shown to outperform alternative strategies in recent simulation studies (Compton et al. 2007; Cushman, McRae, et al. 2013; Diniz et al. 2020; Unnithan Kumar and Cushman 2022; Lumia et al. 2023; Lumia, Modica, Cushman 2024; Lumia, Modica, Praticò et al. 2024). Factorial least-cost path (LCP) analysis (Cushman et al. 2009) can complement this by identifying potential movement routes across landscapes. These approaches have proven effective in identifying core habitat areas vital for population viability, as well as ecological corridors critical for dispersal (Cushman, Landguth, et al. 2013; Cushman et al. 2016; Kaszta, Cushman, Htun, et al. 2020; Kaszta, Cushman, Macdonald, et al. 2020; Haidir et al. 2021; Loveridge et al. 2022). Further refinement in habitat prioritization can be achieved through spatial graph theory. Metrics such as the integral index of connectivity (IIC) enable the ranking of habitat patches and corridors based on their contribution to overall landscape connectivity (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Torné 2009; Saura and Rubio 2010). When combined, these methodologies offer a powerful toolset for identifying conservation priorities that include both core habitats and connecting elements (e.g., Rudnick et al. 2012; Crouzeilles et al. 2013; Cushman et al. 2014; Diniz et al. 2017; Macdonald et al. 2018; Kaszta et al. 2020b).

The snow leopard (*Panthera uncia*), an iconic species of Asia's high mountain ecosystems, is emblematic of their ecological and conservation value (McCarthy et al. 2017). Despite its symbolic importance, significant research gaps remain, especially concerning landscape connectivity (Robinson and Weckworth 2016; Riordan et al. 2016; Li et al. 2020). To address these gaps, recent studies have examined both broad and regional connectivity patterns. Riordan et al. (2016) identified key linkages and barriers across the species' range. Li et al. (2020) defined and mapped connectivity among proposed "landscape conservation units (LCUs)." Regionally, Hameed et al. (2020) modeled habitat and connectivity in Pakistan, Shrestha and Kindlmann (2020) identified corridors between snow leopard sightings in Nepal, and Li et al. (2021) examined potential changes to snow leopard habitats in Qinghai, China, due to climate change, identifying areas of potential stability. In Qilianshan, Li et al. (2022) also analyzed the influence of infrastructure on habitat connectivity, focusing on critical habitats and intermediary pathways. However, with the exception of Li et al. (2020, 2021), few studies have adopted a systematic approach to identify, assess, or rank core habitat zones and ecological corridors as specific conservation targets (Cushman, Landguth, et al. 2013; Cushman et al. 2018; Kaszta et al. 2020b). To design

informed management strategies, is it essential to evaluate and compare the relative importance of core areas and dispersal pathways (Puyravaud et al. 2017; Cushman et al. 2018; Kaszta et al. 2019; Kaszta, Cushman, Htun, et al. 2020; Kaszta, Cushman, Macdonald, et al. 2020), thereby enabling more effective connectivity-based conservation planning.

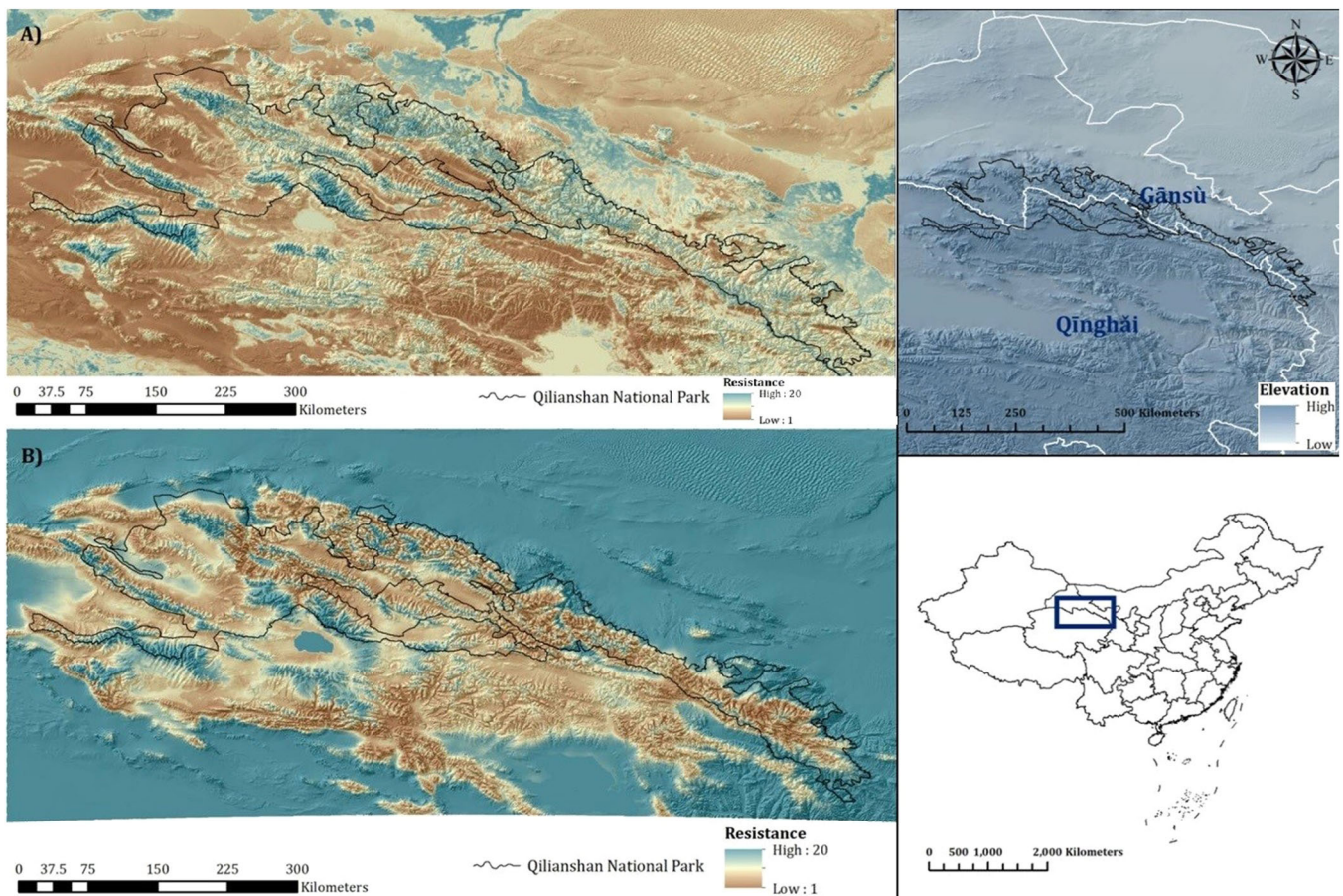
In this study, we assess the newly designated Qilianshan National Park in central China, which spans the provinces of Gansu and Qinghai at the northeastern edge of the Qinghai-Tibetan Plateau, and give recommendations for future improvement. We use this park as a case study to evaluate its effectiveness in protecting snow leopard habitat and supporting landscape connectivity. Our analysis is based on spatially optimized habitat and landscape genetics models developed for the region (Atzeni et al. 2020, 2023), and employs empirically grounded synoptic connectivity modeling methods (Cushman, Landguth, et al. 2013; Cushman et al. 2014; Diniz et al. 2020; Unnithan Kumar and Cushman 2022). We identify core areas critical to snow leopard persistence and map major dispersal corridors. We also apply graph-based analysis to quantify the role of each core area in maintaining network integrity (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Torné 2009) and prioritize conservation actions accordingly.

Finally, we assess the extent to which the current boundaries of Qilianshan National Park effectively protect these key snow leopard habitats and the mountain ecosystems of central China.

## 2 | Methods

### 2.1 | Study Area

Qilianshan National Park (QLSNP) (N 36°29'57"–39°43'39", E 97°23'34"–103°45'49") covers a total area of 50,200 km<sup>2</sup>, spanning multiple administrative jurisdictions across Gansu (34,400 km<sup>2</sup>) and Qinghai (15,800 km<sup>2</sup>) provinces in China (Figure 1). The broader Qilian Mountains (Qilianshan) region comprises high mountain ranges, valleys, and intermontane basins. Elevation in the area mostly exceeds 3000–3500 m above sea level, with an average elevation of approximately 4000 m. The annual average temperature is –4°C, with seasonal extremes ranging from 37.6°C in summer to –35.8°C in winter. Annual precipitation averages around 400 mm. Vegetation types follow a clinal variation along altitude gradient and include mountain grassland (1800–2800 m), temperate shrub steppe (2000–2200 m), mountain forest grassland (2600–3400 m), subalpine shrub meadow (3200–3500 m), and high mountain sparse vegetation (> 3500 m).



**FIGURE 1** | Overview of the study area across the Chinese provinces of Gansu and Qinghai (top right inset) and its position within the PRC (bottom right inset). The main figures show the resistance models adopted in this study. (A) Genetic resistance model, derived extrapolating to the whole extent a genetically optimized resistance model (Atzeni et al. 2023) created upon snow leopard genotypes in Gansu. (B) Habitat-based resistance model, created by applying a negative exponential transformation to the top performing relative suitability model for the whole area from Atzeni et al. (2020). Both resistances have been rescaled in the range 1–20.

## 2.2 | Simulated Points

The best-performing habitat suitability model for the study area, developed by Atzeni et al. (2020), was reclassified according to percentile breaks at the 95th, 85th, and 75th percentiles of relative suitability values, corresponding to high, medium-to-high, and low-to-high habitat quality thresholds, respectively (Supporting Information S2: Figure S1). The area of suitable habitat under each threshold was calculated using a cell-based operation in ArcGIS, both for the total study area and within the boundaries of QLSNP. The chosen suitability model was an ensemble of top-performing models corrected for observation bias using a Gaussian kernel (see Supporting Information S2: Figure S3 and Atzeni et al. [2020] for details).

To simulate connectivity and dispersal patterns across the landscape, a cloud of 100,000 random points was initially generated across the entire study extent. These were then clipped to the area encompassing medium-to-high quality habitat patches, yielding 8528 points representing parts of the landscape most likely to be inhabited by snow leopards based on habitat quality. From this set, five random subsamples of 1000 points each were selected to account for location uncertainty and to evaluate the combined effect of variation in source and destination locations (Supporting Information S2: Figure S2). All connectivity analyses described below were repeated on each of the five random subsets, and the resulting predictions were averaged to produce a final, spatially representative ensemble output.

## 2.3 | Resistance Surfaces

The resistance surfaces used in this study were derived from snow leopard distribution models developed for the Qilianshan region by Atzeni et al. (2020), and from genetically optimized resistance surfaces generated by Atzeni et al. (2023) based on individual genotypes collected in Qilianshan National Park, Gansu Province (see Supporting Information S2: Figure S3 and Supporting Information S1: File S1; sampling details in Atzeni et al. 2021).

The best-performing habitat suitability model generated by Atzeni et al. (2020) for the Qilianshan area was an ensemble of the top 10 models after correction for sampling bias. Common predictors among these models included human footprint variables (road and settlement density), topographic factors (slope position and dissection), climate (temperature), and land cover metrics at both the landscape (aggregation index, patch density) and class levels (area, percentage, and elongation metrics for grassland and shrub land types). Snow leopards were consistently associated with ridges and uplands, avoiding large valley bottoms and areas with high road density, likely due to human disturbance. Preferred landscapes were characterized by high aggregation of dominant land cover types, particularly grasslands that support key prey species, suggesting that spatial configuration and extent of grassland were key habitat selection criteria driven by predatory behavior. Additionally, snow leopards were associated with moderate river density, as these areas provide strategic ambush sites for hunting. Temperature emerged as the strongest predictor, reflecting the species' preference for higher elevations in

Qilianshan, although its effects were intertwined with topographic constraints.

This habitat suitability model was converted to a resistance surface using a negative exponential transformation:

$$10^{(-1 \cdot HS)},$$

where HS represents the habitat suitability scores (Wan et al. 2019) (hereafter referred to as the *habitat-based resistance model*). The exponential transformation, rather than a negative linear one, is generally preferred in studies of connectivity using habitat-based resistance models (Mateo-Sánchez et al. 2015a, 2015b; Keeley et al. 2016, 2017; Zeller et al. 2018). Since factors influencing habitat preference may differ from those influencing dispersal (Wasserman et al. 2010; Elliot et al. 2014; Diniz et al. 2020), this transformation allows dispersal through medium- to low-habitat suitability areas (Mateo-Sánchez et al. 2015a, 2015b; Keeley et al. 2016; Zeller et al. 2018; Diniz et al. 2020) rather than restricting movement to only high-quality habitats.

The best-performing genetically optimized resistance surface was also adopted from Atzeni et al. (2023), based on snow leopard genetic profiles from Gansu (Atzeni et al. 2021) (hereafter referred to as the *genetic resistance model*). This model showed that gene flow in snow leopards is largely facilitated by areas of intermediate ruggedness and elevation, corresponding to small-to-large valleys between mountain ranges, and by areas with intermediate land cover heterogeneity composed of functionally connected land cover types (Atzeni et al. 2023). As the landscape genetics inference covered only a portion of this landscape in Gansu (Atzeni et al. 2021), the resistance surface used in the current analysis was extrapolated using predictors with the same functional relationships identified in Atzeni et al. (2023), allowing us to model resistance across the entire landscape. Incorporating these landscape genetic insights enabled a more refined estimation of functional connectivity, capturing ecological processes beyond habitat preference alone, which may not be reliable proxies for describing genetic flow and dispersal (Atzeni et al. 2023).

Both resistance surfaces were rescaled to a uniform range of 1–20 using the raster transformation tool in SpatialEco (Evans 2020), with a resolution of 500 m to reduce the computational cost (Figure 1).

## 2.4 | Resistant Kernel Modeling

We used UNICOR (Landguth et al. 2012) to calculate cumulative resistant kernels (Compton et al. 2007), based on the habitat-based resistance surface and applying a dispersal threshold equivalent to 25 km. This distance approximates the daily movement capability of snow leopard (McCarthy et al. 2005) and was selected to ensure comprehensive coverage of areas where snow leopards could potentially persist. Given the high number of simulated occurrence points and stochastic replication of dispersal simulations, a 25 km threshold represents an ecologically realistic and conservative estimate of daily

displacement, sufficient for identifying core habitat areas at the landscape level without necessitating larger thresholds. Recent empirical studies on snow leopard movement further support approximation: Johansson et al. (2024) found that dispersing juvenile snow leopards in the Gobi Desert exhibited mean daily displacements of 30.9 km, whereas in mountainous terrain, subadults and adult males covered average daily distances of 4.8 and 7.2 km, respectively (Johansson et al. 2022). Additionally, exploratory forays of juveniles recorded in Johansson et al. (2024) had an average straight-line displacement of 34.98 km over multiple days, further supporting the 25 km threshold as a reasonable approximation of maximum potential displacement, accounting for the nonlinear nature of actual movement paths (Johansson et al. 2016, 2018).

A threshold corresponding to the 85th percentile of the averaged kernel surfaces was chosen to identify core habitat areas, consistent with approaches used in previous studies to identify the fracture zones separating core movement probability patches (Cushman, Landguth, et al. 2013; Cushman et al. 2018; Khosravi et al. 2018; Macdonald et al. 2018; Ashrafzadeh et al. 2020; Kaszta et al. 2020b). The resulting core patches were then analyzed in FRAGSTATS (McGarigal et al. 2012) to compute class-level metrics relevant to landscape connectivity: largest patch index (LPI), number of patches (NP), percentage of landscape (PLAND), area-weighted mean patch size (AREA\_AM), and area-weighted radius of gyration (GYRATE\_AM). PLAND is the simplest metric of landscape composition, quantifying the proportion of total area occupied by the patch class of interest. NP is a simple measure of habitat fragmentation and reports the number of discrete habitat patches in the landscape of a particular patch type. LPI describes the size of the largest patch of a given type relative to the total landscape area (McGarigal et al. 2012; Cushman, Landguth, et al. 2013). GYRATE\_AM represents the average linear distance an animal can travel before leaving a patch when dropped at random on the landscape. AREA\_AM expresses the average patch area conditions that the focal species would experience, randomly located within the landscape. These metrics were selected based on their demonstrated relevance in assessing landscape pattern effects on connectivity (e.g., Wasserman et al. 2012, 2013; Cushman, Shirk, et al. 2013).

The same descriptive indices were calculated for the core areas identified within QLSNP boundaries to quantify the proportion of core habitat currently under protection status versus those extending into adjacent snow leopard range lying outside formal protection. To assess the relative importance of each core patch (relative to the whole extent), we ranked them by the product of patch area and the cumulative kernel values (strength) contained within them, representing their strength and contribution to overall connectivity (Cushman et al. 2018; Kaszta, Cushman, Macdonald, et al. 2020b).

## 2.5 | Contribution of Core Areas to Landscape Connectivity

Conefor 2.6 (Saura and Torné 2009) was used to establish the relative importance of each core area patch within the landscape network topology representing total connectivity. Conefor

relies on a graph-based representation of landscape structure (Pascual-Hortal and Saura 2006), composed of nodes and links that represent patches of suitable habitat and the functional connections between them as a function of distance (Urban and Keitt 2001; Pascual-Hortal and Saura 2006). It quantifies habitat availability indices that simultaneously consider the connectivity within each patch, connectivity among patches, as well as habitat abundance and the overall rate of connectivity (Pascual-Hortal and Saura 2006).

Both resistance models were used to calculate edge-to-edge LCPs between adjacent core areas using the Linkage Pathways tool, implemented in Linkage Mapper (McRae and Kavanagh 2011). For each resistance surface, a matrix of partial least-cost distances was produced, excluding pairwise connections that passed through the allocation zone of a third patch.

The strength of each core patch was used as a node attribute in the graph analyses. Conefor analyses were performed using partial connections and the IIC (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007) to evaluate the contribution of each core patch to the connectivity network. Topologies were evaluated at cost-distance thresholds of 25, 50, 100, 250, and 500 k cost units, and results were reported as the average across these five thresholds (Norris et al. n.d.; Crouzeilles et al. 2013; Diniz et al. 2017). The absolute variation in IIC was used to quantify the importance of each landscape element for overall habitat availability:

$$\text{varIIC} = \frac{\text{IIC} - \text{IIC}'}{\text{IIC}},$$

where IIC' is the index value after removal of a specific patch, and IIC is the value with the patch present (Saura and Torné 2009). varIIC can be partitioned into three fractions, each representing a different way in which a patch contributes to landscape connectivity (Saura and Rubio 2010; Bodin and Saura 2010):

$$\text{varIIC} = \text{varIIC}_{\text{intra}} + \text{varIIC}_{\text{flux}} + \text{varIIC}_{\text{connector}}.$$

The fraction varIIC<sub>intra</sub> (Intra) measures intra-patch connectivity (i.e., patch strength), independent of how a patch is connected to others. varIIC<sub>flux</sub> (Flux) quantifies the attribute-weighted dispersal flux through the connections of a given patch, as either the origin or destination of a connection. The last fraction, varIIC<sub>connector</sub> (Connector), measures the patch's topological importance as a stepping-stone between other patches; it is independent of patch attributes and indicates the role of the patch in maintaining overall network cohesion (Saura and Rubio 2010). We also computed the metric BC(IIC), a generalization of the betweenness centrality (BC) index (Freeman 1977), which considers patch attributes and topological distances, and assigns more importance to patches expected to support higher fluxes and connect larger, more ecologically important patches. Finally, for both resistance scenarios, we calculated  $C(50)_k^{\text{IIC}}$  (Bodin and Saura 2010), an index that identifies the minimum number of patches needed to compensate for > 50% of connectivity loss (as measured by BC(IIC)) following the removal of any given patch.

## 2.6 | Factorial LCP Modeling

The analyses described above rely exclusively on edge-to-edge patch least-cost distances between adjacent core areas and do not provide information on the relative importance of links within the network topology, nor on how these may vary under different resistance models. To address this, we employed the factorial LCP (FLCP) approach (Cushman et al. 2009), implemented in UNICOR (Landguth et al. 2012). FLCPS were calculated for each of the five random draws of points, using a 1000 km-equivalent threshold (the largest dispersal threshold used in Riordan et al. 2016), to model landscape-level dispersal pathways likely to span multiple snow leopard generations (e.g., Kaszta et al. 2020b). Corridors were smoothed with a 10 km width, and the outputs were averaged across the five sets of occurrence points. Pearson's correlation coefficients were computed between the resistance scenarios to quantify their level of agreement, using the Band Collection Statistics Tool in ArcGIS. FLCP rasters from both scenarios were reclassified using the 95th percentile of the value distribution in each raster. Corridor fragments were then extracted, isolating all paths lying outside the core habitat patches. The reclassified outputs were used to calculate the following metrics in FRAGSTATS: LPI, NP, AREA\_AM, and GYRATE\_AM at the class level, and AREA and GYRATE at the patch level (McGarigal et al. 2012). These same metrics were calculated for corridors falling within the boundaries of the national park to evaluate the proportion and magnitude of connectivity links located outside protected areas.

The importance of each corridor (across the entire extent) was ranked using the product of three factors: the shape and length of the corridor, the sum of LCP intensity values within the corridor (Kaszta et al. 2019, 2020b), and the average strength of the intersected core kernel patches (Cushman et al. 2018; Kaszta et al. 2020b), calculated within a 10 km radius. This approach accounts for routes in close proximity to core areas and helps address location uncertainty in predicted dispersal routes.

**TABLE 1** | Proportion of habitat categories (in km<sup>2</sup>) and summary statistics for the resistant kernel core patches, both calculated on the total extent and inside Qilianshan National Park (QLSNP).

	Habitat classes	Total (km <sup>2</sup> )	QLSNP (km <sup>2</sup> )	Park/Total
<b>Habitat quality</b>	High	15,716.00	6,767.00	0.43
	Medium-to-high	47,148.00	17,769.00	0.38
	Low-to-high	78,580.00	27,010.00	0.34
	Metrics	Total	QLSNP	Park/Total
<b>Kernel patches</b>	PLAND	15.00	37.73	NA
	NP	92.00	64.00	0.70
	LPI	3.61	12.97	NA
	Gyrate_Am (km)	41.11	34.88	0.85
	Area_Am (km <sup>2</sup> )	5,898.78	3,438.70	0.58
	Total area (km <sup>2</sup> )	47,154.50	18,935.50	0.40

*Note:* Where applicable, a ratio between the proportion of the metrics inside QLSNP and the whole extent has been calculated. Habitat classes have been inferred re-categorizing the predicted relative habitat suitability surface (Atzeni et al. 2020) according to the 75th, 85th, and 95th percentile of raster values distribution for low-to-high, medium-to-high, and high-quality habitat, respectively. Kernel core area patches derive from reclassification of the Resistant Kernel raster according to the 85th percentile of raster values distribution. Metrics relative to the Kernel patches have the following meaning: Area\_Am, class area area-weighted mean; Gyrate\_Am, class area-weighted mean radius of gyration; LPI, largest patch index; NP, number of patches; PLAND, percentage of landscape; total area, area of all patches.

## 3 | Results

### 3.1 | Habitat Extent and Resistant Kernel Core Areas

Re-categorization of the habitat surface from Atzeni et al. (2020) yielded a total area of suitable snow leopard habitat amounting to 15,716 km<sup>2</sup> (high quality), 41,148 km<sup>2</sup> (medium-to-high quality), and 78,580 km<sup>2</sup> (low-to-high quality) (Table 1). The corresponding proportions of these habitat classes within QLSNP were 6767 km<sup>2</sup> (43.1% of the total), 17,769 km<sup>2</sup> (37.7% of the total), and 27,010 km<sup>2</sup> (34.4% of the total), respectively. The total area encompassed by resistant kernel-derived core habitat patches was 47,154.5 km<sup>2</sup> (Table 1). Of this, 18,935.5 km<sup>2</sup>—or 40.2%—fell within QLSNP boundaries (Table 1). The proportion of core kernel patches relative to QLSNP's total area (PLAND) was 37.72% (Table 1), and these patches represented 69.6% of the total number of core patches identified. Core areas within QLSNP were generally smaller in area (AREA\_AM) and had shorter average dispersal radii (GYRATE\_AM) than those across the full study extent (Table 1). QLSNP accounted for 58.3% of the total average patch area conditions (AREA\_AM) and 84.8% of the average radius of gyration (GYRATE\_AM), relative to the full extent (Table 1). The 25 most important core areas identified via resistant kernel analysis were all larger than 100 km<sup>2</sup> (Supporting Information S2: Figure S4, Supporting Information S2: Table S1).

### 3.2 | Core Area Importance to Network Connectivity

The contribution of core areas to intra-patch connectivity (Intra) reflected the strength values of the kernel patches (Supporting Information S2: Figure S4, Supporting Information S2: Table S1). As such, patches characterized by greater strength also facilitated the majority of intra-patch snow leopard movement. The most important patches were located in the

northwestern portion of the study area (Patch 1; counties of Subei, Sunan, and Tianjun), the south (Patch 2; Delingha and Tianjun), the southeast (Patch 3; Sunan, Qilian, and Menyuan), and the central region (Patches 4, 5, and 6; Qilian, Sunan, Gangca, and Tianjun) (Supporting Information S2: Figure S4).

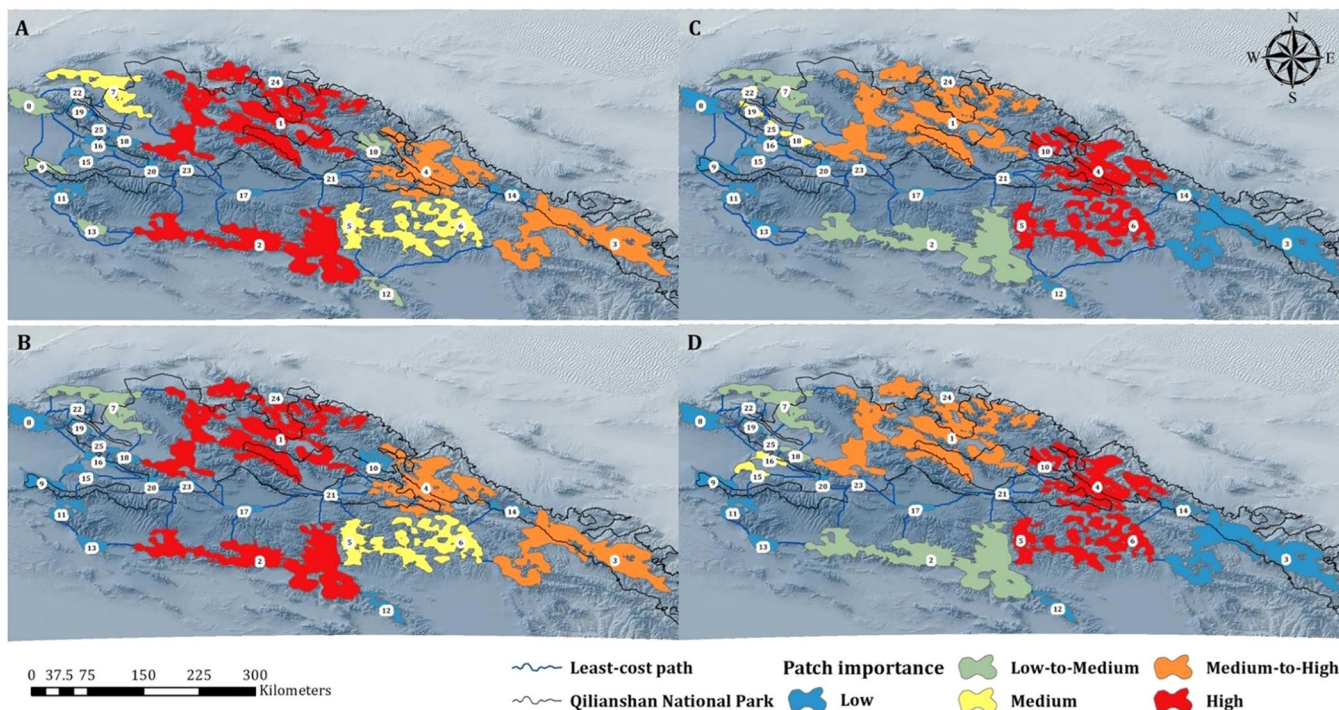
Flux results were largely consistent between the resistance models for patches 1 through 6 (Figure 2A,B). Differences in this metric arose from variation in the LCP patterns between adjacent core areas (Figure 2), with the genetic model highlighting greater snow leopard flux centered around patches 7, 8, 9, 10, and 12, compared to the habitat-based model. The Connector fraction showed general agreement between the two resistance scenarios, underscoring the critical role of patches 4, 5, 6, and 10 in maintaining overall network connectivity (Figure 2C,D). Minor differences involved smaller patches acting as stepping stones in the northwestern portion of the study area, with their contributions depending on the specific LCPs between adjacent core areas.

We compared the normalized values of the Connector fraction and the BC(IIC) metric, following the interpretation scheme from Bodin and Saura (2010) to assess patch importance (Figure 3). Both resistance scenarios consistently indicated that patches 4, 5, and 6 constitute central core areas ensuring connectivity across the entire network, as also reflected in their  $C(50)^{IIC}$  values of 0, 1, and 2, respectively (Figure 3). Similarly, the loss of patch 10, critical to maintaining connectivity within QLNSP (Figure 2), would require at least three other patches for functional compensation (Figure 3).

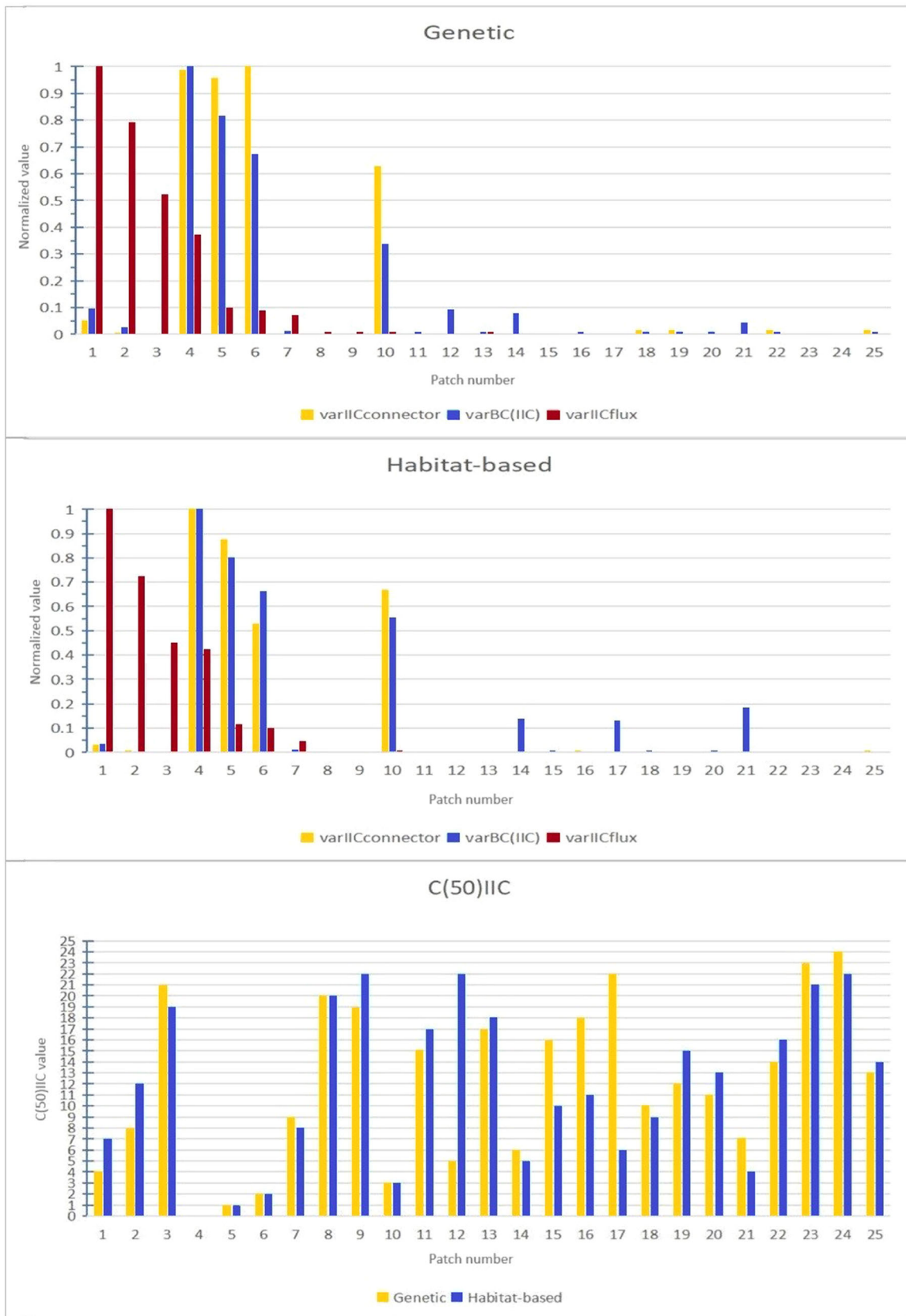
While other stepping-stone patches had negligible influence on overall network integrity, higher BC(IIC) values were observed in the genetic resistance model for patches 12, 15, and 21, and in the habitat-based model for patches 14, 17, and 21. Compensation requirements ( $C(50)^{IIC}$ ) for these patches varied between resistance scenarios (Figure 3). Notably, patches 1–3, which were most important for intra-patch connectivity and dispersal flux, generally had lower rankings for Connector and BC(IIC) metrics (Figure 3). An exception was patch 1, which had the fifth highest Connector score and relatively high BC(IIC) values, especially under the genetic resistance model (Figure 3).

### 3.3 | Factorial LCP Corridors and Patterns

The number of corridor fragments was higher under the habitat-based resistance scenario, both across the full extent of the study area and within QLSNP (Table 2), although both scenarios revealed that approximately 50% of dispersal routes were located inside the National Park. On average, corridors identified in the habitat-based scenario were shorter (GYRATE\_AM) and smaller (AREA\_AM) than those derived from the genetic scenario. The average corridor radius of gyration (GYRATE\_AM) decreased substantially within QLSNP boundaries, representing 55% (habitat-based) and 27% (genetic-based) of the total. Likewise, the average corridor area (AREA\_AM) within QLSNP was smaller than the overall average, amounting to 44% and 24% of the total for habitat-based and genetic scenarios, respectively (Table 2).



**FIGURE 2** | Results from the Conefor analysis showing the importance of the 25 top kernel core area patches according to the varIICflux fraction (A) genetic model; (B: habitat-based model) and the varIICconnector fraction (C) genetic model; (D: habitat-based model). The results represent the average values across five thresholds of least-cost distance (25, 50, 100, 250, and 500 k cost units). Least-cost paths between adjacent core areas from either scenario are displayed to illustrate connections between patches and highlight differences between scenarios. Patch numbering follows the rank of the varIICintra fraction (i.e., “Strength” of core areas; Supporting Information S2: Table S1).



**FIGURE 3** | Comparison between the normalized varIICconnector, varBC(IIC), and varIICflux fractions for each core area patch in either resistance scenario (top: genetic resistance model; middle: habitat-based resistance model), together with the values of C(50)IIC (bottom) for the two resistance scenarios.

**TABLE 2** | Summary statistics of corridors fragments, inferred through the factorial least-cost path algorithm, connecting the 25 most important kernel core area patches.

Metrics	Total		QLSNP		Park/Total	
	Habitat	Genetic	Habitat	Genetic	Habitat	Genetic
NP	234.00	107.00	117.00	59.00	0.50	0.55
LPI	9.52	19.87	10.16	25.81	Not applicable	
Gyrate_Am (km)	10.49	51.40	5.72	14.06	0.55	0.27
Area_Am (km <sup>2</sup> )	224.86	1856.82	100.01	439.79	0.44	0.24
Total gyrate (km)	509.36	544.81	207.83	188.08	0.41	0.35
Total area (km <sup>2</sup> )	6538.00	13,806.00	2480.00	3782.50	0.38	0.27

*Note:* These corridors have been obtained by re-classifying the factorial least-cost path outputs according to the 95th percentile of raster values distribution and refer to factorial least-cost paths lying outside any given core area. These metrics compare the habitat-based resistance model (Habitat) to the genetic resistance model (Genetic). Where applicable, a ratio between the proportion of the metrics inside Qilianshan National Park (QLSNP) and the whole extent has been calculated. Metrics have the following meaning: Area\_Am, class area area-weighted mean; Gyrate\_Am, class area-weighted mean radius of gyration; LPI, largest patch index; NP, number of patches; Total area, area of all patches; Total Gyrate, sum of the radius of gyration of all patches.

Across the entire study area, the genetic scenario produced 13,806 km<sup>2</sup> of corridors, while the habitat-based scenario resulted in 6538 km<sup>2</sup> of corridors connecting core areas. Within QLSNP, the total area covered by corridors dropped considerably relative to the whole extent, representing 38% of the total for the habitat-based scenario and 27% for the genetic scenario (Table 2).

The factorial LCP surfaces revealed notable differences between the resistance models (Figure 4), exemplified by a low correlation (Pearson's  $r = 0.083$ ). In general, the major factorial LCPs in the habitat-based scenario followed conditions strictly associated with habitat, such as ridgelines and fine-scale topographic depressions in high mountain systems. Conversely, the major factorial LCPs in the genetic scenario ran through broad, flat open areas at the base of mountain ranges.

We identified and highlighted the 15 most important corridors for each resistance scenario (Figure 4; Supporting Information S2: Table S2). The two scenarios revealed that a large proportion of the strongest links were located outside QLSNP: corridors 1, 2, 4, 5, 6, 7, 10, 11, and 13 in the habitat-based scenario; and corridors 1, 2, 3, 6, 7, 8, 11, 13, 14, and 15 in the genetic scenario.

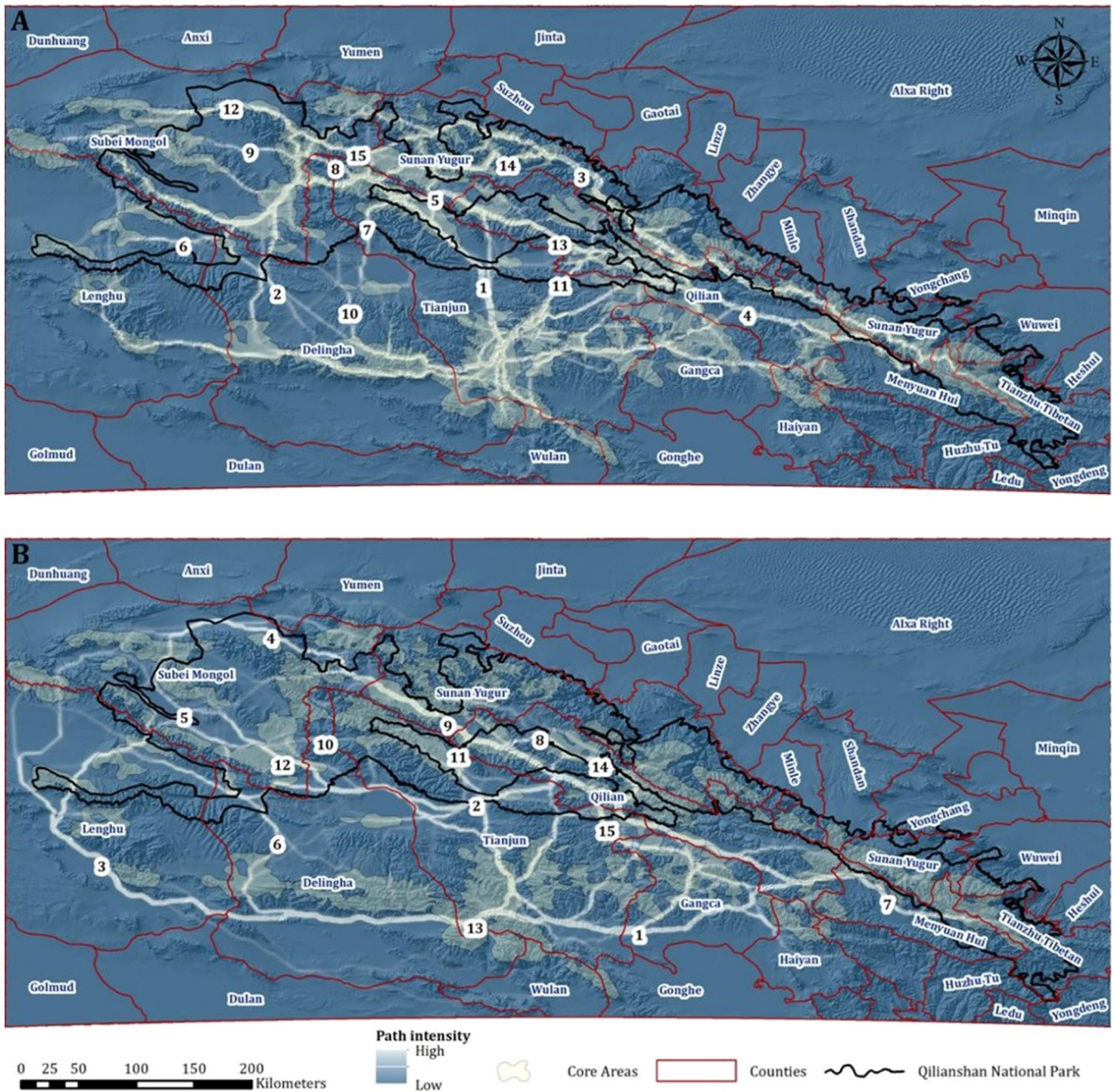
## 4 | Discussion

### 4.1 | Conservation Management

This application of synoptic connectivity methods, coupled with a graph-based analysis, highlighted that a significant portion of the Qilianshan landscape is important for overall regional connectivity, yet much of it lies outside the currently designated protected area. From a conservation management perspective, it is therefore important to accurately assign priority to areas of interest to inform the development of management plans and assess the potential for their inclusion within the official boundaries of the protected area. We intend for the results of this analysis to serve as a tool to guide and improve monitoring efforts and inform future park planning initiatives.

The varIICconnector (Connector) and BC(IIC) metrics capture different aspects of a patch's role in maintaining overall connectivity. Loss of a patch with a high Connector value would result in an immediate and significant reduction in network connectivity (such patches are considered more "irreplaceable"). In contrast, patches with lower Connector values are less irreplaceable, but if they also have a high BC(IIC) score, their loss would necessitate substantial reworking of dispersal pathways through alternative patches to maintain connectivity. For this reason, Bodin and Saura (2010) recommend using the BC(IIC) metric to complement varIICconnector in identifying priority areas and facilitating decision-making (Figure 3). Based on these guidelines, our analysis highlights five key areas, with strong consensus between models. Patches 4, 5, 6, and 10 all scored highest on both metrics, with minimal order variation between the two models. These are followed by patch 1, which had much lower scores for both Connector and BC(IIC), but ranked highest on the Flux metric. These areas should be prioritized to support and enhance connectivity across the Qilianshan region, especially patches 5 and 6, which lie entirely outside of the currently defined National Park. Additionally, it is interesting to note that for patches 4, 10, and 1, although much of their extent is within the protected area, a substantial portion of their area still falls outside the park's boundaries. Recent findings support prioritizing these patches for further attention and potential inclusion in National Park management. For example, Atzeni et al. (2021), through analysis of genetic diversity structure in the western Gansu portion of QLSNP, found higher genetic diversity, heterozygosity, and effective population size in areas encompassed by patch 1.

Similarly, our mapping of corridors connecting these patches found a significant number lie outside the current National Park boundaries, in both modeling scenarios. In each case, many corridors located in Delingha and Tianjun counties functionally connect core areas in the northwestern and central regions (within QLSNP) to unprotected habitat patches in the southern portion (e.g., corridors 1 and 2 in the habitat-derived scenario, and corridors 1, 2, and 6 in the genetic-derived scenario; Figure 4). Other important corridors in either scenario linked the southeastern parts of the park to the southern core habitat areas (e.g., corridors 3 and 4 in the habitat-derived scenario; Figure 4).



**FIGURE 4** | Factorial least-cost path intensity surfaces, calculated upon a dispersal ability of 1000 km-equivalent. All corridors derive from a reclassification of the factorial least-cost path raster according to the 95th percentile of the raster values distribution. This figure illustrates the 15 most important linkages (A) habitat-based model; (B: genetic model), ranked in order according to the product between the length attribute, the sum of the factorial least-cost path values inside each corridor, and the average strength of core areas intersecting the corridors within a radius of 10 km. County-level administrative levels have been overlaid to assist with the geographic localization and prospective management of these major dispersal pathways.

Particularly noteworthy are the long dispersal corridors identified in the genetic resistance model, running through the counties of Gangca, Tianjun, Delingha, and Lenghu. These suggest potential landscape-level dispersal routes connecting the southeastern part of the study area to habitat patches located in the northwest, which could benefit from additional protection (e.g., corridors 1, 3, and 13 in the genetic-derived scenario; Figure 4). Additionally, the differing habitat features prioritized in each scenario underscore an important consideration for conservation management planning: in addition to protecting what are generally seen as

“optimal” habitats for movement (e.g., ridgelines), the inclusion of less “optimal” habitat features (e.g., flat areas at the foot of mountain ranges) may also be critical for effectively protecting animal dispersal between habitat patches (Johansson et al. 2024).

After the park’s establishment in October 2018, the Qilianshan National Park Qinghai Provincial Administration and the Gansu Provincial Administration were organized, dividing management of QLSNP between them, with overarching coordination by the National Forestry and Grassland Bureau

(Forestry and Grassland Bureau 2019). The National Park is zoned into two sections: a core protected area and a general control area, which align with IUCN categories Ia-Ib and II, respectively (QLSNP Masterplan 2018). A framework for annual evaluation and adjustment has been established, with 2025 designated as the first major review milestone of the full national park system (QLSNP Masterplan 2018; Xinhua News Agency 2019). These milestones present a valuable opportunity to review studies such as ours, apply findings to develop more targeted and effective monitoring strategies, reassess existing boundaries, and consider strategic expansions of the National Park.

## 4.2 | Qilianshan in Overall Conservation

Ensuring support and protection of connectivity in the Qilianshan area holds additional implications for range-wide conservation of snow leopard populations. Facilitating connectivity between snow leopard populations in China and Mongolia may be of particular significance, as these two groups have been shown to be genetically distinct (Janecka et al. 2017; Hacker et al. 2023), with limited landscape connectivity between them (Riordan et al. 2016).

The geographic location of Qilianshan places it at a critical junction, potentially linking important snow leopard habitats in northern China with those in southern Mongolia. This is supported by several recent analyses. Norris et al. (n.d.) identified the QLSNP area as part of a key linkage connecting the Tibetan Plateau to southern Mongolia and recommended expanding the level and extent of protection. Li et al. (2020) designated the Qilianshan region as a major LCU with links to the southern Tibetan Plateau and the Hengduan, south Gobi, and central Tianshan-Pamir-Hindu Kush-Karakorum LCUs. Riordan et al. (2016) described the Gobi Desert region as an important area for connectivity, with potential stepping-stones and corridors extending toward Qilianshan. Qilianshan may thus represent the last stopover or the first encounter with “optimal” habitat for snow leopards attempting to cross, or having just crossed the Gobi Desert during dispersal. Johansson et al. (2024) observed snow leopards crossing large expanses of flat steppe as they moved south from the Mongolian Tost Mountains toward China, with one individual appearing to follow the LCP delineated by Li et al. (2020) linking to the Qilianshan region—although its movement was impeded by linear infrastructure (border fencing).

Ongoing monitoring and adequate protection of the Qilianshan area are also important for maintaining snow leopard habitat in the face of global climatic change. The high mountain regions of Asia, including the Tibetan Plateau, have warmed at more than twice the average rate of the Northern Hemisphere, posing additional challenges for the persistence of threatened snow leopard populations (Liu and Chen 2000; Chen et al. 2009; Forrest et al. 2012). Climate refugia—areas with relatively stable climate and complex landscape topography—can serve as retreat zones for species under severe climate pressure (Ashcroft 2010; Morelli et al. 2016). Li et al. (2016) identified Qilianshan as one of three large-scale climate refugia capable of supporting snow leopard adaptation and persistence under ongoing climate change conditions.

## 4.3 | Comparison of Resistance Surfaces

Our results show that connectivity predictions inferred through a habitat-based resistance scenario differ from those generated using a genetically optimized resistance surface. This provides further confirmation that these scenarios reflect different ecological processes—the former aligns with factors that maximize fitness within home ranges, while the latter reflects landscape characteristics that facilitate dispersal and mating behavior—as also noted in previous studies (Spear et al. 2010; Wasserman et al. 2010; Cushman, McRae, et al. 2013; Mateo-Sánchez et al. 2015a, 2015b). Mateo-Sánchez et al. (2015a) also observed differences in effective distances derived from such models, suggesting that habitat-derived surfaces may overestimate resistance in areas characterized by low habitat suitability.

Our models from Qilianshan confirm this observation. In the habitat-based resistance scenario, major connectivity routes were identified within core patches, while movement pathways outside these areas were largely governed by patterns of habitat suitability (Atzeni et al. 2020; Figure 4). This is unsurprising, as both core patches and habitat-based dispersal routes were derived from the same resistance scenario, reflecting well-documented relationships between snow leopards and landscape characteristics that influence home-range selection (Atzeni et al. 2020). Because these corridors reflected suitable habitat extent, they resulted in more fragmented and smaller links beyond core areas when compared with those inferred by the genetic resistance model, which was not constrained by habitat suitability (Table 2; Supporting Information S2: Table S2).

By contrast, the genetic resistance surface—largely dominated by fine-scale ruggedness and elevation (Atzeni et al. 2023)—identified flatter areas within a suitable elevation range as primary conduits for gene flow (Figure 4). However, this model tended to overestimate effective distances within home-range patches (Figure 4). It is therefore appropriate to adopt an integrated connectivity map (Zeller et al. 2017, 2018), one that incorporates both fine-scale movement within home ranges and long-distance connectivity patterns related to dispersal. Such a map would reflect a multitemporal pattern of population connectivity, integrating short-term movement dynamics with long-term demographic and genetic exchange across the broader landscape.

Differences in connectivity patterns are common when comparing models based on different data types or modeling approaches (Cushman and Lewis 2010; Cushman et al. 2014; Shirk et al. 2015; Zeller et al. 2018; Hearn et al. 2019). In this study, beyond the ecological phenomena represented by the two data types, differing patterns also stem from the use of distinct suites of variables (Cushman and Lewis 2010; Hearn et al. 2019) and from the extrapolation of results from a limited area to a broader extent (Cushman and Lewis 2010; Wasserman et al. 2012). The two models were based on different ecological assumptions and employed different topographical and land cover predictors (Atzeni et al. 2020, 2023). Additionally, the genetic resistance was developed from data limited to Gansu Province (Atzeni et al. 2021, 2023), making it particularly sensitive to the landscape characteristics pertinent to the northwestern portion of the study area, whereas the habitat-based resistance model was derived from data collected across the entire National Park (Atzeni et al. 2020).

To enhance comparability between connectivity patterns, future research should aim to use the same set of predictors and conduct analyses across a consistent spatial extent (Cushman and Lewis 2010; Hearn et al. 2019), whether focusing on home-range selection or drivers of gene flow. In addition, direct monitoring of snow leopard dispersal via GPS-collared individuals would aid in the optimization (e.g., Elliot et al. 2014) and validation (e.g., Finerty et al. 2023) of the resistance surfaces and connectivity models developed here. Moving forward, studies can build on these findings by incorporating additional empirical data across the entire study area under consideration (e.g., genetic data, presence or density data from camera trapping, presence or movement data from GPS and telemetry, etc.), while adequately accounting for detection bias and expanding the scope of landscape variables, including prey availability and human presence and disturbance.

## 5 | Conclusions

The evidence generated by this analysis highlights that the QLSNP protected area, in its current form, may be inadequate to ensure protection of regional snow leopard habitat connectivity, especially when set in a meta-population context. The framework we adopted has the advantage of providing a synoptic representation of connectivity patterns by integrating complementary approaches, and it differs from previous range-wide and local studies by explicitly ranking major core habitat areas and identifying the spatial location of the most important stepping-stones and movement corridors. This objective ranking of both core patches and factorial LCPs makes it possible to tailor conservation strategies. Identifying and protecting major core areas, and the most important dispersal routes linking them, should be prioritized to ensure meta-population viability and reduce the risk of isolation for large carnivores.

The results from this study may prompt further sampling and monitoring efforts and help guide management initiatives aimed at evaluating new areas for legal protection that are currently outside the extent of the National Park. Such actions could functionally connect the Qilianshan landscape to other important snow leopard strongholds. Future improvements should incorporate threats posed by anthropogenic factors, such as human activity and population, linear infrastructure, grazing pressure, and may also include information on natural prey populations, which are an essential factor for the persistence of viable snow leopard populations.

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### Author Contributions

**Aliana Norris:** data curation, formal analysis, methodology, writing – original draft, writing – review and editing. **Samuel A. Cushman:** conceptualization, methodology, supervision, writing – review and editing. **Jun Wang:** formal analysis. **Philip Riordan:** conceptualization; supervision; writing – review and editing. **Kun Shi:** conceptualization, funding acquisition, supervision. **Hua Zhong:** data curation. **Luciano Atzeni:** conceptualization, data curation, formal analysis, methodology, supervision, visualization, writing – original draft, writing – review and editing.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The distribution model and resistance surfaces adopted in this study are considered sensitive data by the National Forestry and Grassland Administration of China (NFGA). As such, limitations on the free distribution of this data apply. The corresponding author welcomes inquiry about the use of our resistance and distribution models in related frameworks focusing on snow leopard conservation in the Qilianshan landscape.

### References

- Andersen, L. W., V. Harms, R. Caniglia, et al. 2015. “Long-Distance Dispersal of a Wolf, *Canis lupus*, in Northwestern Europe.” *Mammal Research* 60: 163–168.
- Ashcroft, M. B. 2010. “Identifying Refugia From Climate Change.” *Journal of Biogeography* 37: 1407–1413.
- Ashrafzadeh, M. R., R. Khosravi, M. A. Adibi, A. Taktehrani, H. Y. Wan, and S. A. Cushman. 2020. “A Multi-Scale, Multi-Species Approach for Assessing Effectiveness of Habitat and Connectivity Conservation for Endangered Felids.” *Biological Conservation* 245: 108523.
- Atzeni, L., S. A. Cushman, D. Bai, et al. 2020. “Meta-Replication, Sampling Bias, and Multi-Scale Model Selection: A Case Study on Snow Leopard (*Panthera uncia*) in Western China.” *Ecology and Evolution* 10: 7686–7712.
- Atzeni, L., S. A. Cushman, J. Wang, P. Riordan, K. Shi, and D. Bauman. 2021. “Evidence of Spatial Genetic Structure in a Snow Leopard Population From Gansu, China.” *Heredity* 127: 522–534.
- Atzeni, L., J. Wang, P. Riordan, K. Shi, and S. A. Cushman. 2023. “Landscape Resistance to Gene Flow in a Snow Leopard Population From Qilianshan National Park, Gansu, China.” *Landscape Ecology* 38: 1847–1868.
- Baguette, M., S. Blanchet, D. Legend, V. M. Stevens, and C. Turlure. 2013. “Individual Dispersal, Landscape Connectivity and Ecological Networks.” *Biological Reviews* 88: 310–326.
- Bodin, Ö., and S. Saura. 2010. “Ranking Individual Habitat Patches as Connectivity Providers: Integrating Network Analysis and Patch Removal Experiments.” *Ecological Modelling* 221: 2393–2405.
- Chen, F., J. Wang, L. Jin, Q. Zhang, J. Li, and J. Chen. 2009. “Rapid Warming in Mid-Latitude Central Asia for the Past 100 Years.” *Frontiers of Earth Science in China* 3: 42–50.
- Compton, B. W., K. McGarigal, S. A. Cushman, and L. R. Gamble. 2007. “A Resistant-Kernel Model of Connectivity for Amphibians That Breed in Vernal Pools.” *Conservation Biology* 21: 788–799.
- Crouzeilles, R., M. L. Lorini, and C. E. V. Grelle. 2013. “The Importance of Using Sustainable Use Protected Areas for Functional Connectivity.” *Biological Conservation* 159: 450–457.

- Cushman, S., J. Lewis, and E. Landguth. 2014. "Why Did the Bear Cross the Road? Comparing the Performance of Multiple Resistance Surfaces and Connectivity Modeling Methods." *Diversity* 6: 844–854.
- Cushman, S. A., N. B. Elliot, D. Bauer, et al. 2018. "Prioritizing Core Areas, Corridors and Conflict Hotspots for Lion Conservation in Southern Africa." *PLoS One* 13: e0196213.
- Cushman, S. A., N. B. Elliot, D. W. Macdonald, and A. J. Loveridge. 2016. "A Multi-Scale Assessment of Population Connectivity in African Lions (*Panthera leo*) in Response to Landscape Change." *Landscape Ecology* 31: 1337–1353.
- Cushman, S. A., E. L. Landguth, and C. H. Flather. 2013. "Evaluating Population Connectivity for Species of Conservation Concern in the American Great Plains." *Biodiversity and Conservation* 22: 2583–2605.
- Cushman, S. A., and J. S. Lewis. 2010. "Movement Behavior Explains Genetic Differentiation in American Black Bears." *Landscape Ecology* 25: 1613–1625.
- Cushman, S. A., K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. "Gene Flow in Complex Landscapes: Testing Multiple Hypotheses With Causal Modeling." *American Naturalist* 168: 486–499.
- Cushman, S. A., K. S. McKelvey, and M. K. Schwartz. 2009. "Use of Empirically Derived Source-Destination Models to Map Regional Conservation Corridors." *Conservation Biology* 23: 368–376.
- Cushman, S. A., B. McRae, F. Adriaensen, P. Beier, M. Shirley, and K. Zeller. 2013. "Biological Corridors and Connectivity First Edit." In *Key Topics in Conservation Biology*, edited by D. W. Macdonald and K. J. Willis, 2, 384–404. John Wiley & Sons, Ltd.
- Cushman, S. A., A. J. Shirk, and E. L. Landguth. 2013. "Landscape Genetics and Limiting Factors." *Conservation Genetics* 14: 263–274.
- Diniz, M. F., S. A. Cushman, R. B. Machado, and P. De Marco Júnior. 2020. "Landscape Connectivity Modeling From the Perspective of Animal Dispersal." *Landscape Ecology* 35: 41–58.
- Diniz, M. F., R. B. Machado, A. A. Bispo, and D. Brito. 2017. "Identifying Key Sites for Connecting Jaguar Populations in the Brazilian Atlantic Forest." *Animal Conservation* 21: 201–210.
- Elliot, N. B., S. A. Cushman, D. W. Macdonald, and A. J. Loveridge. 2014. "The Devil Is in the Dispersers: Predictions of Landscape Connectivity Change With Demography." *Journal of Applied Ecology* 51: 1169–1178.
- Evans, J. 2020. *spatialEco. R Package Version 1.3-1*.
- Fattebert, J., T. Dickerson, G. Balme, R. Slotow, and L. Hunter. 2013. "Long-Distance Natal Dispersal in Leopard Reveals Potential for a Three-Country Metapopulation." *South African Journal of Wildlife Research* 43: 61–67.
- Finerty, G. E., S. A. Cushman, D. T. Bauer, et al. 2023. "Evaluating Connectivity Models for Conservation: Insights From African Lion Dispersal Patterns." *Landscape Ecology* 38: 3205–3219.
- Forestry and Grassland Bureau. 2019. "The National Forestry and Grassland Administration Released the Pilot Results of the Northeast Tiger and Leopard National Park, the Qilian Mountain, and Giant Panda National Park." [https://www.gov.cn/xinwen/2019-10/12/content\\_5438719.htm](https://www.gov.cn/xinwen/2019-10/12/content_5438719.htm).
- Forrest, J. L., E. Wikramanayake, R. Shrestha, et al. 2012. "Conservation and Climate Change: Assessing the Vulnerability of Snow Leopard Habitat to Treeline Shift in the Himalaya." *Biological Conservation* 150: 129–135.
- Frankham, R. 2005. "Genetics and Extinction." *Biological Conservation* 126: 131–140.
- Freeman, L. C. 1977. "A Set of Measures of Centrality Based on Betweenness." *Sociometry* 40: 35–41.
- Gilpin, M., and M. Soule. 1986. "Minimum Viable Populations: Processes of Species Extinction." In *Conservation Biology: The Science of Scarcity and Diversity*, edited by M. Soule, 19–34. Sinauer.
- Gray, C. L., S. L. L. Hill, T. Newbold, et al. 2016. "Local Biodiversity Is Higher Inside Than Outside Terrestrial Protected Areas Worldwide." *Nature Communications* 7: 12306.
- Hacker, C., L. Atzeni, B. Munkhtsog, et al. 2023. "Genetic Diversity and Spatial Structures of Snow Leopards (*Panthera uncia*) Reveal Proxies of Connectivity Across Mongolia and Northwestern China." *Landscape Ecology* 38: 1013–1031.
- Haidir, I. A., Ž. Kaszta, L. L. Sousa, M. I. Lubis, D. W. Macdonald, and M. Linkie. 2021. "Felids, Forest and Farmland: Identifying High Priority Conservation Areas in Sumatra." *Landscape Ecology* 36: 475–495.
- Hameed, S., J. Din, H. Ali, et al. 2020. "Identifying Priority Landscapes for Conservation of Snow Leopards in Pakistan." *PLoS One* 15: e0228832.
- Hearn, A. J., S. A. Cushman, B. Goossens, et al. 2019. "Predicting Connectivity, Population Size and Genetic Diversity of Sunda Clouded Leopards Across Sabah, Borneo." *Landscape Ecology* 34: 275–290.
- Janecka, J. E., Y. Zhang, D. Li, et al. 2017. "Range-Wide Snow Leopard Phylogeography Supports Three Subspecies." *Journal of Heredity* 108: 597–607.
- Johansson, Ö., J. S. Alexander, P. Lkhagvajav, C. Mishra, and G. Samelius. 2024. "Natal Dispersal and Exploratory Forays Through Atypical Habitat in the Mountain-Bound Snow Leopard." *Ecology* 105: e4264.
- Johansson, Ö., G. Koehler, G. R. Rauset, et al. 2018. "Sex-Specific Seasonal Variation in Puma and Snow Leopard Home Range Utilization." *Ecosphere* 9: e02371.
- Johansson, Ö., C. Mishra, G. Chapron, et al. 2022. "Seasonal Variation in Daily Activity Patterns of Snow Leopards and Their Prey." *Scientific Reports* 12: 21681.
- Johansson, Ö., G. R. Rauset, G. Samelius, et al. 2016. "Land Sharing Is Essential for Snow Leopard Conservation." *Biological Conservation* 203: 1–7.
- Kaszta, Ž., S. A. Cushman, A. J. Hearn, et al. 2019. "Integrating Sunda Clouded Leopard (*Neofelis diardi*) Conservation Into Development and Restoration Planning in Sabah (Borneo)." *Biological Conservation* 235: 63–76.
- Kaszta, Ž., S. A. Cushman, S. Htun, H. Naing, D. Burnham, and D. W. Macdonald. 2020. "Simulating the Impact of Belt and Road Initiative and Other Major Developments in Myanmar on an Ambassador Felid, the Clouded Leopard, *Neofelis nebulosa*." *Landscape Ecology* 35: 727–746.
- Kaszta, Ž., S. A. Cushman, and D. W. Macdonald. 2020. "Prioritizing Habitat Core Areas and Corridors for a Large Carnivore Across Its Range." *Animal Conservation* 23: 607–616.
- Keeley, A. T. H., P. Beier, and J. W. Gagnon. 2016. "Estimating Landscape Resistance From Habitat Suitability: Effects of Data Source and Nonlinearities." *Landscape Ecology* 31: 2151–2162.
- Keeley, A. T. H., P. Beier, B. W. Keeley, and M. E. Fagan. 2017. "Habitat Suitability Is a Poor Proxy for Landscape Connectivity During Dispersal and Mating Movements." *Landscape and Urban Planning* 161: 90–102.
- Khosravi, R., M. R. Hemami, and S. A. Cushman. 2018. "Multispecies Assessment of Core Areas and Connectivity of Desert Carnivores in Central Iran." *Diversity and Distributions* 24: 193–207.
- Landguth, E. L., B. K. Hand, J. Glassy, S. A. Cushman, and M. A. Sawaya. 2012. "UNICOR: A Species Connectivity and Corridor Network Simulator." *Ecography* 35: 9–14.
- Li, J., T. M. McCarthy, H. Wang, et al. 2016. "Climate Refugia of Snow Leopards in High Asia." *Biological Conservation* 203: 188–196.
- Li, J., B. V. Weckworth, T. M. McCarthy, et al. 2020. "Defining Priorities for Global Snow Leopard Conservation Landscapes." *Biological Conservation* 241: 108387.
- Li, J., Y. Xue, C. E. Hacker, et al. 2021. "Projected Impacts of Climate Change on Snow Leopard Habitat in Qinghai Province, China." *Ecology and Evolution* 11: 17202–17218.

- Li, Y., Y. Zhang, Y. Xue, et al. 2022. "Analysis of Conservation Gaps and Landscape Connectivity for Snow Leopard in Qilian Mountains of China." *Sustainability* 14: 1638.
- Liu, X., and B. Chen. 2000. "Climatic Warming in the Tibetan Plateau During Recent Decades." *International Journal of Climatology* 20: 1729–1742.
- Loveridge, A. J., L. L. Sousa, S. Cushman, Ž. Kaszta, and D. W. Macdonald. 2022. "Where Have All the Lions Gone? Establishing Realistic Baselines to Assess Decline and Recovery of African Lions." *Diversity and Distributions* 28: 2388–2402.
- Lumia, G., S. A. Cushman, S. Pratico, and G. Modica. 2023. "Intra-Network Analysis Based on Comparison Between Graph Theory Approach and Pathwalker." *Computational Science and its Applications - ICCSA 2023 Workshops, ICCSA 2023, Lecture Notes in Computer Science*, Vol. 14107, 300–309. Springer.
- Lumia, G., G. Modica, and S. Cushman. 2024. "Using Simulation Modeling to Demonstrate the Performance of Graph Theory Metrics and Connectivity Algorithms." *Journal of Environmental Management* 352: 120073.
- Lumia, G., G. Modica, S. Praticò, and S. Cushman. 2024. "Comparison of Patch-Based and Synoptic Connectivity Algorithms With Graph Theory Metrics. A Case Study in Reggio Calabria Metropolitan Area (South Italy)." *Ecological Informatics* 82: 102678.
- Macdonald, E. A., S. A. Cushman, E. L. Landguth, A. J. Hearn, Y. Malhi, and D. W. Macdonald. 2018. "Simulating Impacts of Rapid Forest Loss on Population Size, Connectivity and Genetic Diversity of Sunda Clouded Leopards (*Neofelis diardi*) in Borneo." *PLoS One* 13: e0196974.
- Mateo-Sánchez, M. C., N. Balkenhol, S. Cushman, T. Pérez, A. Domínguez, and S. Saura. 2015a. "Estimating Effective Landscape Distances and Movement Corridors: Comparison of Habitat and Genetic Data." *Ecosphere* 6: 1–16.
- Mateo-Sánchez, M. C., N. Balkenhol, S. Cushman, T. Pérez, A. Domínguez, and S. Saura. 2015b. "A Comparative Framework to Infer Landscape Effects on Population Genetic Structure: Are Habitat Suitability Models Effective in Explaining Gene Flow?" *Landscape Ecology* 30: 1405–1420.
- McCarthy, T. M., T. K. Fuller, and B. Munkhtsog. 2005. "Movements and Activities of Snow Leopards in Southwestern Mongolia." *Biological Conservation* 124: 527–537.
- McCarthy, T. M., D. Mallon, R. Jackson, et al. 2017. *Panthera uncia*. <https://www.iucnredlist.org>.
- McGarigal, K., S. A. Cushman, and E. Ene. 2012. *FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps*. Computer Software Program Produced by the Authors at the University of Massachusetts, Amherst.
- McRae, B., and D. Kavanagh. 2011. *Linkage Mapper Connectivity Analysis Software*. The Nature Conservancy.
- Morelli, T. L., C. Daly, S. Z. Dobrowski, et al. 2016. "Managing Climate Change Refugia for Climate Adaptation." *PLoS One* 11: e0159909.
- Norris, A. C., P. Riordan, S. A. Cushman, K. Shi, and L. Atzeni. n.d. "Identifying Priority Areas to Guide Management Planning of a Protected Area Network to Support Snow Leopard (*Panthera uncia*) in Asia." *Journal to Ecological Solutions and Evidence*. In press.
- Palomares, F., M. Delibes, P. Ferreras, J. M. Fedriani, J. Calzada, and E. Revilla. 2000. "Iberian Lynx in a Fragmented Landscape: Predispersal, Dispersal, and Postdispersal Habitats." *Conservation Biology* 14: 809–818.
- Pascual-Hortal, L., and S. Saura. 2006. "Comparison and Development of New Graph-Based Landscape Connectivity Indices: Towards the Prioritization of Habitat Patches and Corridors for Conservation." *Landscape Ecology* 21: 959–967.
- Puyravaud, J.-P., S. A. Cushman, P. Davidar, and D. Madappa. 2017. "Predicting Landscape Connectivity for the Asian Elephant in Its Largest Remaining Subpopulation." *Animal Conservation* 20: 225–234.
- QLSNP Masterplan. 2018. "Qilian Shan National Park Masterplan." <http://www.forestry.gov.cn/qls/3/index.html>.
- Riordan, P., S. A. Cushman, D. Mallon, K. Shi, and J. Hughes. 2016. "Predicting Global Population Connectivity and Targeting Conservation Action for Snow Leopard Across Its Range." *Ecography* 39: 419–426.
- Robinson, H., and B. Weckworth. 2016. "Landscape Ecology: Linking Landscape Metrics to Ecological Processes." In *Snow Leopards. Biodiversity of the World: Conservation From Genes to Landscapes*, edited by T. McCarthy, D. Mallon, and P. Nyhus, 395–405. Academic Press.
- Rudnick, D., S. Ryan, P. Beier, S. Cushman, F. Dieffenbach, and S. Trombulak. 2012. "The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities." *Issues Ecology* 16: 1–20.
- Saura, S., and L. Pascual-Hortal. 2007. "A New Habitat Availability Index to Integrate Connectivity in Landscape Conservation Planning: Comparison With Existing Indices and Application to a Case Study." *Landscape and Urban Planning* 83: 91–103.
- Saura, S., and L. Rubio. 2010. "A Common Currency for the Different Ways in Which Patches and Links Can Contribute to Habitat Availability and Connectivity in the Landscape." *Ecography* 33: 523–537.
- Saura, S., and J. Torné. 2009. "Conefor Sensinode 2.2: A Software Package for Quantifying the Importance of Habitat Patches for Landscape Connectivity." *Environmental Modelling & Software* 24: 135–139.
- Shirk, A. J., M. A. Schroeder, L. A. Robb, and S. A. Cushman. 2015. "Empirical Validation of Landscape Resistance Models: Insights From the Greater Sage-Grouse (*Centrocercus urophasianus*)." *Landscape Ecology* 30: 1837–1850.
- Shrestha, B., and P. Kindlmann. 2020. "Implications of Landscape Genetics and Connectivity of Snow Leopard in the Nepalese Himalayas for Its Conservation." *Scientific Reports* 10: 19853.
- Spear, S. F., N. Balkenhol, M.-J. Fortin, B. H. McRae, and K. Scribner. 2010. "Use of Resistance Surfaces for Landscape Genetic Studies: Considerations for Parameterization and Analysis." *Molecular Ecology* 19: 3576–3591.
- Stoner, C., T. Caro, S. Mduma, C. Mlingwa, G. Sabuni, and M. Borner. 2007. "Assessment of Effectiveness of Protection Strategies in Tanzania Based on a Decade of Survey Data for Large Herbivores." *Conservation Biology* 21: 635–646.
- Tischendorf, L., and L. Fahrig. 2000. "On the Usage and Measurement of Landscape Connectivity." *Oikos* 90: 7–19.
- Unnithan Kumar, S., and S. A. Cushman. 2022. "Connectivity Modelling in Conservation Science: A Comparative Evaluation." *Scientific Reports* 12: 16680.
- Urban, D., and T. Keitt. 2001. "Landscape Connectivity: A Graph-Theoretic Perspective." *Ecology* 82: 1205–1218.
- Wan, H. Y., S. A. Cushman, and J. L. Ganey. 2019. "Improving Habitat and Connectivity Model Predictions With Multi-Scale Resource Selection Functions From Two Geographic Areas." *Landscape Ecology* 34: 503–519.
- Wang, D., H. Hao, H. Liu, L. Sun, and Y. Li. 2023. "Dynamic Change of Habitat Quality and Its Key Driving Factors in Ningxia Hui Autonomous Region, China." *Nature Conservation* 53: 125–155.
- Wasserman, T. N., S. A. Cushman, J. S. Littell, A. J. Shirk, and E. L. Landguth. 2013. "Population Connectivity and Genetic Diversity of American Marten (*Martes americana*) in the United States Northern Rocky Mountains in a Climate Change Context." *Conservation Genetics* 14: 529–541.
- Wasserman, T. N., S. A. Cushman, M. K. Schwartz, and D. O. Wallin. 2010. "Spatial Scaling and Multi-Model Inference in Landscape Genetics: *Martes americana* in Northern Idaho." *Landscape Ecology* 25: 1601–1612.
- Wasserman, T. N., S. A. Cushman, A. S. Shirk, E. L. Landguth, and J. S. Littell. 2012. "Simulating the Effects of Climate Change on

Population Connectivity of American Marten (*Martes americana*) in the Northern Rocky Mountains, USA.” *Landscape Ecology* 27: 211–225.

Van der Weyde, L. K., C. Mbisana, and R. Klein. 2018. “Multi-Species Occupancy Modelling of a Carnivore Guild in Wildlife Management Areas in the Kalahari.” *Biological Conservation* 220: 21–28.

Xinhua News Agency. 2019. *A Guideline on Establishing a Protected Area System With National Parks As Its Mainstay*. General Office of the Central Committee of the Communist Party of China and General Office of the State Council.

Zeller, K. A., M. K. Jennings, T. W. Vickers, H. B. Ernest, S. A. Cushman, and W. M. Boyce. 2018. “Are All Data Types and Connectivity Models Created Equal? Validating Common Connectivity Approaches With Dispersal Data.” *Diversity and Distributions* 24: 868–879.

Zeller, K. A., T. W. Vickers, H. B. Ernest, and W. M. Boyce. 2017. “Multi-Level, Multi-Scale Resource Selection Functions and Resistance Surfaces for Conservation Planning: Pumas as a Case Study.” *PLoS One* 12: e0179570.

### Supporting Information

Additional supporting information can be found online in the Supporting Information section.

**Supplementary Table S1:** Summary statistics of the 25 most important kernel core area patches, ranked by the ‘Strength’ attribute, obtained as the product of their area and the sum of kernel intensity values contained in each patch **Supplementary Table S2:** Summary statistics of the 15 top factorial least-cost path corridors, ranked by the ‘Weighted LCP strength’ attribute, obtained as the product of their length (‘LCP length’), sum of movement intensity values contained in each corridor (‘LCP sum’), and the average strength of core areas intersecting the corridors within a radius of 10 km (‘Average Kernel strength’). **Supplementary Figure S1:** Habitat quality classes following the re-classification of the top performing snow leopard relative habitat suitability model created on this extent (Atzeni et al. 2020). **Supplementary Figure S2:** An example of one among the five probable snow leopard locations (1000 points each) used to model potential within home-range movement and long-distance dispersal through the resistant kernel and the factorial least-cost path algorithms. **Supplementary Figure S3:** Step by step flow chart for the conceptualization and execution of this analysis, including use of previously published data. **Supplementary Figure S4:** Resistant Kernel movement probability surface, calculated upon a 25 km-equivalent omnidirectional movement ability. **Species distribution modeling for snow leopards in Qilianshan (Atzeni et al. 2020) review. Genetic optimization of resistance surfaces for snow leopards in Qilianshan (Atzeni et al. 2023) review.**