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Three Decades of Habitat Loss and Northward Shift in the Red-Crowned Crane on the Songnen Plain: Conservation Gaps and the Need for Network Expansion

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Abstract

The red-crowned crane (*Grus japonensis*) is a flagship species for wetland biodiversity in East Asia. The Songnen Plain is a vital wetland and habitat for rare and endangered birds in Northeast China. However, rapid land use changes have raised urgent concerns about habitat loss and the survival of these populations. We combined 30 years (1990–2020) of field surveys with ensemble species distribution models (SDMs) to analyze the spatio-temporal changes in suitable habitats for all three key life stages—spring migration, breeding, and autumn migration—across the Songnen Plain. We also assessed how well the current protected-area (PA) network covers suitable habitats and identified conservation gaps. Land use type was the most significant predictor of habitat suitability. Over this period, suitable habitats decreased sharply by 60% (spring migration), 72% (breeding), and 76% (autumn migration), with severe fragmentation and a clear northward shift. Core suitable areas are now mainly found within a few nature reserves, including Zhalong, Wuyu'er River, and Xianghai. We identified three significant conservation gaps: Lindian–Anda, Tailai–Dumeng, and Meilisi Daur–Fuyu. Our results show widespread habitat reduction and demonstrate the inadequacy of the current PA network in supporting the long-term survival of red-crowned crane populations. We recommend expanding protections and restoring wetland connectivity within these gaps to maintain critical habitats and improve landscape resilience for this endangered species.

Keywords: red-crowned crane (*Grus japonensis*); species distribution models (SDMs); habitat fragmentation; wetland loss; protected-area gaps; Songnen Plain

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1. Introduction

China is one of the most biodiverse countries in the world, yet its biodiversity faces serious threats [1,2]. Major causes of these changes include habitat degradation or complete loss due to overexploitation of natural resources and climate change caused by excessive human activities [3,4]. For birds, habitat must provide abundant food sources, suitable nesting sites, and shelter from predators and harsh weather to ensure their survival and successful reproduction [5–7]. Habitat selection and use have long been central, important,

and challenging themes in animal ecology [8,9], and they remain vital methods for studying rare and endangered species and conserving biodiversity [10].

The red-crowned crane is a large wading bird that mainly inhabits open wetlands, marshes, lakes, and riverbanks [11]. It is a typical long-distance migrant, with breeding grounds mostly in the Russian Far East and the wetlands of Northeast China. Its wintering areas include the middle and lower reaches of the Yangtze River in China, the Korean Peninsula, and Japan. The species is listed as Vulnerable (VU) on the IUCN Red List (2025-1). In Chinese culture, the red-crowned crane symbolizes longevity and good fortune; it is also revered as the "god of wetlands" and serves as a flagship species of wetland ecosystems with significant ecological and cultural importance [12–14]. The species mainly inhabits East Asia and is divided into insular and continental populations [15]. The insular population, found in Hokkaido, Japan, is non-migratory, while the continental population is further divided into eastern and western migratory groups. The current global wild population is estimated at roughly 3430 individuals, of which about 1900 belong to the insular group [16,17]. Conservation of the red-crowned crane remains challenging; the insular population exhibits significantly lower genetic diversity compared to its continental counterparts [18]. Additionally, rising temperatures, changes in precipitation, and increasing extreme climate events directly impact migration routes, habitat choice, and food sources [18,19]. Human activities such as agricultural expansion, wetland reclamation, and urbanization continue to fragment and destroy crane habitats [20]. Landscape changes, especially wetland fragmentation and declining habitat quality, threaten the species' survival [21].

The Songnen Plain is a crucial habitat and stopover point for the red-crowned crane, forming a central part of the East Asian-Australasian Flyway [22]. As migratory birds, cranes have complex, fluctuating habitat requirements that vary over time and by location [23]. Since the mid-1980s, extensive agricultural expansion in the Songnen Plain has caused ongoing land use shifts. The large-scale exploitation of land resources has resulted in ecological degradation, ecosystem disruption, and significant land use changes, which negatively impact red-crowned crane populations [24,25]. Habitat loss and environmental decline are widely acknowledged as primary causes of species endangerment and pose serious threats to biodiversity [26]. Empirical studies indicate that landscape fragmentation and habitat destruction directly speed up extinction rates among wild species [27,28]. Consequently, ecological changes in the Songnen Plain have become a key focus in wetland and landscape ecology, given its importance as a vital breeding ground and migration stopover for the red-crowned crane.

Against this backdrop, we hypothesize that, driven by extensive agricultural expansion from 1990 to 2020, suitable habitats for the red-crowned crane in the Songnen Plain have significantly decreased in size and become more fragmented at higher latitudes. Additionally, the current protected-area network does not include all core breeding, spring migration, and autumn migration habitats, leading to notable conservation gaps.

2. Materials and Methods

2.1. Study Area and Study Design

The Songnen Plain is situated in the central-western part of Northeastern China. It was formed by sediment deposition from the Songhua and Nen Rivers and their tributaries. The Nen and Songhua Rivers flow through the southwestern part of the plain and eventually terminate as inland, "beheaded" rivers that create a closed drainage basin. The plain lies within the Songnen Basin and includes marginal mountainous areas, low hills, piedmont sloping plains, terraces, plains, and low plains [29]. In this study, the Songnen Plain is defined as the area bounded by the front edge of the hilly terraces and the piedmont sloping

plains, covering roughly 94,260.28 km^2 (Figure 1). The region experiences a temperate continental monsoon climate with four distinct seasons [30]. The average annual temperature is approximately 4 °C, and annual precipitation varies from 270 to 500 mm [31,32].

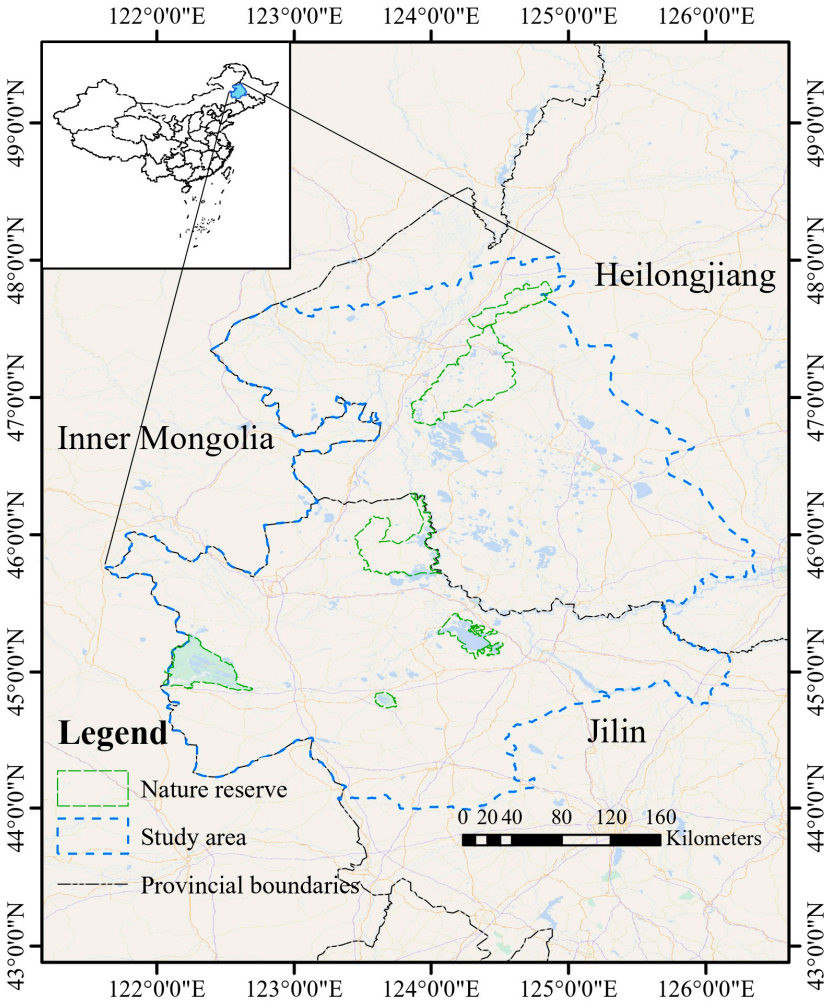


Figure 1. Location of the study area.

The marshes and wetlands of the Songnen Plain are essential habitats for many wild plants and animals, including the red-crowned crane, hooded crane (*Grus monacha*), Siberian crane (*Grus leucogeranus*), and great bustard (*Otis tarda*) [33]. From an expert point of view, these marsh wetlands have been officially protected as nature reserves and Ramsar sites to preserve ecological balance and conserve biodiversity, serving as critical refuges for endangered and rare species. Notable examples include the Zhalong National Nature Reserve and the Wuyu'er River National Nature Reserve in Heilongjiang Province, as well as the Momoge and Xianghai National Nature Reserves in Jilin Province.

2.2. Methods and Data Analysis

Red-crowned crane occurrence records from 1990 to 2000 were obtained from reserve archives or expert consultations; those from 2010 to 2020 were collected through our field surveys, supplemented when necessary, by references [34–37]. In line with red-crowned crane seasonal habitat use, line transect, continuous observation, synchronous observation, and fixed-point methods were employed to gather simultaneous, ongoing data on crane sightings and habitat features within each study area. During spring and autumn migration, 2–3 field surveys were conducted, each lasting 15–20 days. Surveys were carried out daily from 04:00 to 17:00 [12,38]. Observers used binoculars and spotting scopes to locate cranes,

and each sighting was georeferenced with a handheld GPS to record latitude and longitude. All occurrence records (from line transects, fixed-point counts, synchronous censuses, the literature, and expert validation) were first converted to binary presence/absence data within 30 km grid cells to standardize sampling methods before being input into MaxEnt [39]. Breeding season data were collected in Heilongjiang Zhalong National Nature Reserve. By observing incubation behavior through line transect and fixed-point surveys, the entry of red-crowned cranes into the nesting period was confirmed. Nests attended by incubating or brooding adults were located and georeferenced in the field using a handheld GPS [40]. Our field data were collected within four protected areas and extrapolated to the entire Songnen Plain using MaxEnt 3.4.1.

Species distribution models (SDMs) are widely used in wildlife conservation as key tools for understanding how species change their geographic ranges in response to environmental shifts [12,41,42]. Among these, the MaxEnt model offers high predictive accuracy and performance without needing a strict minimum sample size [43,44]. Based on prior research and the characteristics of the Songnen Plain study area, we selected environmental variables by calculating the variance inflation factor (VIF) and removing those with high multicollinearity (VIF $\geq$ 3) [39]. We identified seven ecological variables that affect red-crowned crane habitat selection: altitude, slope, aspect, Normalized Difference Vegetation Index (NDVI), land use (habitat type), distance from cropland, and distance from roads [39,45,46]. All raster variables—NDVI and distances to cropland or roads—were derived from Landsat images captured in 1990, 2000, 2010, and 2020, processed uniformly. The land use classification system used in this study was based on the National Fundamental Resources and Environment Remote Sensing Survey Database (LU2000), completed by the Chinese Academy of Sciences in 2000, and was adjusted to accurately reflect the conditions of the Songnen Plain (Table 1).

Table 1. Landscape pattern index and ecological significance and area of land use types in Songnen Plain from 1990 to 2020.

Land Use Type	Description	Area (km^2)			
		1990	2000	2010	2020
Cropland	Land used for growing crops	42,223.93	43,466.75	44,952.89	46,878.3
Forest land	Includes closed forest, broad-leaved forest, shrubland, sparse woodland, and other wooded land	3126.54	4763.32	8417.96	7248.04
Grassland	Land where herbaceous vegetation covers $\geq$ 5%	16,574.46	14,918.31	9182.77	7535.79
Water body	Natural inland waters and land for water-engineering facilities	8127.46	6642.05	4528.58	4182.13
Built-up land	Urban, rural, and industrial/mining sites plus transportation land outside county towns	3901	5527.65	7011.39	9047.19
Saline–alkali land	Land with surface salt/alkali accumulation, sparse vegetation, and only salt-tolerant plants	8708.82	7144.24	9192.46	10,129.27
Marshland	Flat, poorly drained land that is wet seasonally or permanently and supports hygrophytic vegetation	7638.89	7874.87	5696.75	5910.77
Unused land	Land not currently utilized, mainly sandy land	3959.18	3923.1	5277.49	3328.81

The NDVI was calculated from Landsat imagery, and land use types of the Songnen Plain were identified from these images. Four Landsat datasets were obtained from the Geospatial Data Cloud (http://www.gscloud.cn/), managed by the Computer Network Information Center of the Chinese Academy of Sciences. Topographic variables, including altitude, slope, and aspect, were derived from the same source. The Digital Elevation Model (DEM) data used to describe the topography of the study area were also obtained from the Geospatial Data Cloud website (ASTERGDEM, with a 30 m spatial resolution). Roads

include expressways, national highways, provincial highways, county roads, rural roads, and railways. After digitizing the road network, a Euclidean distance function was used to create a continuous distance raster layer from the road data. Cropland patches were first extracted from the LULC layer using the "Extract by Attributes" tool in ArcGIS 10.4, then a Euclidean distance raster from cropland was generated. All raster and vector layers were standardized in ArcGIS 10.4, projected to the UTM/WGS-1984 coordinate system, resampled to 30 m resolution, and clipped to the boundary of the Songnen Plain (Table 2).

Table 2. Environmental variables used for MaxEnt habitat modeling.

Variable(s)	Spatial Resolution	Temporal Coverage	Data Source
Altitude	30 m	1990–2020	http://www.gscloud.cn/
Slope	30 m	1990–2020	http://www.gscloud.cn/
Aspect	30 m	1990–2020	http://www.gscloud.cn/
NDVI	30 m	1990–2020	Landsat-8 OLI SR
Land use type	30 m	1990–2020	http://www.gscloud.cn/
Distance from cropland	30 m	1990–2020	https://www.webmap.cn/
Distance from road	30 m	1990–2020	https://www.webmap.cn/

MaxEnt software was used to model habitat selection by red-crowned cranes during spring, breeding, and autumn migrations. First, occurrence records of red-crowned cranes and the seven environmental layers were imported into MaxEnt. Among these, land use was treated as a categorical variable, while the remaining predictors were set as continuous. The occurrence data were randomly divided into a 75% training set for model calibration and a 25% test set for independent evaluation. Models were run with the bootstrap option and replicated 10 times, using the "random seed" setting so that a different random subset of occurrence points was selected for each replicate. Model performance was assessed by the area under the receiver operating characteristic curve (AUC) [39,47–49].

The model was set to output in logistic format, generating ASCII raster layers with suitability indices from 0 to 1. The MaxEnt results were imported into GIS for reclassification and visualization. Suitability was classified as follows: not suitable (0–0.25), low suitable (0.25–0.50), moderately suitable (0.50–0.75), and highly suitable (0.75–1.00) [50,51]. Using red-crowned crane distribution data and ArcGIS, we applied the MaxEnt model to map suitable habitats across the Songnen Plain for 1990–2020. A gap analysis was performed to identify conservation gaps during spring migration, autumn migration, and the breeding season. By overlaying the study area with existing protected area maps, we identified spatial gaps and conservation voids [52].

3. Results

3.1. Analysis of Influencing Factors on Red-Crowned Crane Habitat Selection

AUC test values in species distribution models for all periods exceeded 0.94, indicating excellent predictive accuracy. From 1990 to 2020, the distance from cropland and land use type (habitat type) were the most critical environmental variables influencing red-crowned crane habitat selection during spring migration, followed by altitude (Table 3). Logistic results showed that red-crowned cranes are more likely to occur in swamp habitats, occasionally use cropland, and actively avoid roads, which are the main landscape features (Figure 2a). Land use type consistently remained the dominant factor during the breeding season, with distance from cropland and roads ranking second and third, respectively (Table 3). Red-crowned cranes heavily rely on swamp land for nesting. The effect of distance from roads was significant up to approximately 400 m, beyond which it was not significant (Figure 2b). During autumn migration, the primary factors influencing habitat

selection were distance from roads, land use type, and distance from cropland (Table 3). Red-crowned cranes strongly depend on marshland and cropland, followed by grassland, while actively avoiding areas near roads (Figure 2c).

Table 3. Environmental factors determined MaxEnt models estimated species distribution, and their contributions.

Variables	Percent Contribution (%)											
	Spring Migration Period				Breeding Season				Autumn Migration Period			
	1990	2000	2010	2020	1990	2000	2010	2020	1990	2000	2010	2020
Distance from cropland	43.14	60.68	2.71	39.80	28.76	71.31	1.13	48.47	0.12	1.96	11.15	61.86
Type of land use	35.83	16.65	62.21	52.33	61.5	14.51	62.04	43.84	13.76	24.68	45.48	18.71
Normalized Difference Vegetation Index	0.59	9.47	7.78	1.52	0.95	4.61	4.73	1.33	24.25	12.04	10.93	10.54
Aspect	0.62	1.61	0.35	0.39	2.12	1.01	0.25	0.19	0.83	0.49	0.62	0.70
Distance from road	8.32	1.66	10.08	1.66	1.21	2.55	20.85	3.41	36.40	38.38	12.16	6.86
Altitude	11.28	9.67	16.46	3.77	2.24	1.66	9.70	1.80	23.71	22.11	18.37	1.20
Slope	0.22	0.25	0.42	0.53	3.23	4.35	1.29	0.95	0.93	0.34	1.28	0.13

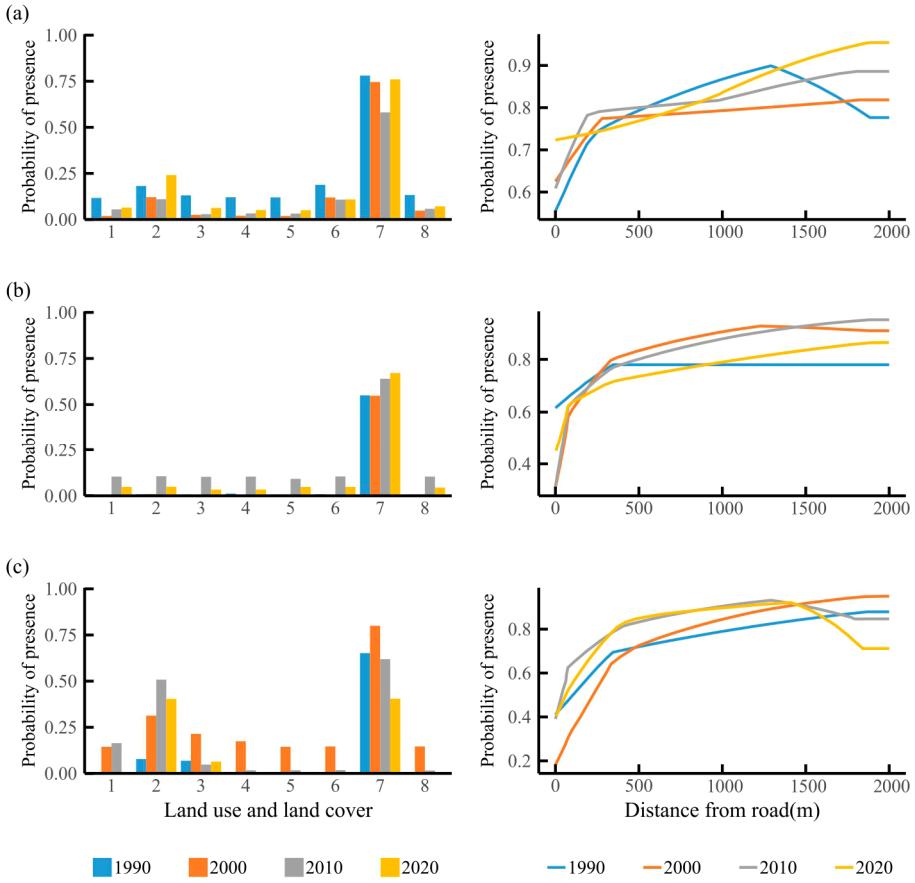


Figure 2. Response curves for land use types and their distance from roads in the habitat selection models (1–8 represent construction land, cropland, grassland, saline-alkali land, forest land, water area, swamp land, and unused land, respectively). (**a**) Response curves during the spring migration period. (**b**) Response curves during the breeding season. (**c**) Response curves during the autumn migration period.

3.2. Spatial-Temporal Changes in the Distribution of Suitable Red-Crowned Crane Habitat

Based on the habitat distribution outputs generated by MaxEnt, we quantified the total area and the area of each suitability class for red-crowned crane habitat across the

Songnen Plain (Figure 3). During the spring migration period, the highly suitable habitat area slightly increased from 1990 to 2000 and then steadily declined, reaching 2193.83 km^2 (0.95% of the study area) in 1990 and only 751.83 km^2 (0.33%) in 2020; the moderately and low suitable habitats increased from 1990 to 2000, sharply dropped in 2010, and continued to decline afterward (Table 4). During the breeding season, the highly suitable habitat area marginally increased from 1990 to 2000 and then decreased steadily, totaling 677.56 km^2 (0.72%) in 1990 and just 133.72 km^2 (0.14%) in 2020; the moderately suitable habitats declined continuously, losing 1748.41 km^2 over the past 30 years, while the low suitable habitats increased significantly from 1990 to 2000 before dropping sharply (Table 4). During the autumn migration period, suitable habitats for the red-crowned crane were heavily reduced, with notable changes in area, proportion, and spatial configuration; the highly suitable habitat area slightly increased from 1990 to 2000 and then continuously declined, amounting to 1970.32 km^2 in 1990 and only 356.01 km^2 in 2020; the moderately and low suitable habitats fluctuated but generally decreased, increasing from 1990 to 2000 before sharply declining (Table 4).

Table 4. Area (km^2) and percentage of suitable habitats for red-crowned cranes.

	Suitability Classification	1990		2000		2010		2020	
		Aera (km^2)	%	Aera (km^2)	%	Aera (km^2)	%	Aera (km^2)	%
Spring Migration Period	Highly suitable	2193.83	0.95	2565.80	1.11	1075.21	0.46	751.83	0.33
	Moderately suitable	7944.91	3.43	9298.98	4.02	4416.53	1.91	3270.03	1.41
	Low suitable	7999.04	8.49	9078.76	9.63	3656.28	3.88	2165.32	2.30
	Not suitable	201,532.85	87.13	197,157.35	85.24	216,836.32	93.75	221,964.80	95.96
Breeding Season	Highly suitable	677.56	0.72	826.77	0.88	457.85	0.49	133.72	0.14
	Moderately suitable	2504.83	2.66	2510.81	2.66	1579.12	1.68	756.42	0.80
	Low suitable	3891.09	4.13	7622.31	8.09	2400.68	2.55	941.45	1.00
	Not suitable	87,185.99	92.49	85,977.02	91.21	89,822.63	95.29	92,428.70	98.06
Autumn Migration Period	Highly suitable	1970.32	0.85	2271.90	0.98	1087.81	0.47	356.01	0.15
	Moderately suitable	5691.14	2.46	7934.97	3.43	3248.71	1.40	1485.89	0.64
	Low suitable	14,135.26	6.11	17,094.88	7.39	8704.91	3.76	2404.96	1.04
	Not suitable	209,503.28	90.58	203,998.25	88.20	218,258.57	94.36	227,053.14	98.16

Suitable habitat is a key factor for population stability. In this study, any habitat with a suitability index above 0.5 was classified as suitable, and the potential suitable habitat area for the red-crowned crane across different periods was measured. During spring migration, the extent of suitable habitats showed alternating expansion and contraction between 1990 and 2020 (Figure 4a). In the breeding season, from 1990 to 2020, suitable habitats shifted from large areas in the northern and southwestern Songnen Plain to a narrower range in the northwestern and far-southwestern edges (Figure 4b). During autumn migration, over the same period, suitability decreased from widespread coverage across the plain to two narrow corridors in the northwest and southwest. Suitable habitats accounted for 2.98% of the study area, while lost habitat was 4.45% (Figure 4c).

3.3. Conservation Gap Analysis of Suitable Red-Crowned Crane (Grus japonensis) Habitat

The Songnen Plain is a vital migration and breeding habitat for the red-crowned crane. Currently, Heilongjiang Province has 37 protected areas covering 8835.25 km^2, while Jilin Province has around 10 protected areas totaling 3483.93 km^2. Notable conservation successes have been achieved in Fuyu and Dorbod counties in Heilongjiang and in Zhenlai and Tongyu counties in Jilin, with significant contributions from Zhalong, Wuyuer River, Xianghai, and Momoge National Nature Reserves. By mapping the spatial distribution of existing protected areas and comparing them with suitable habitat maps generated by MaxEnt for the crane's spring migration, breeding, and autumn migration stages, three

conservation gaps are identified in the Songnen Plain: Lindian–Anda, Tailai–Dorbod, and Meilisi Daur–Fuyu (Figure 5).

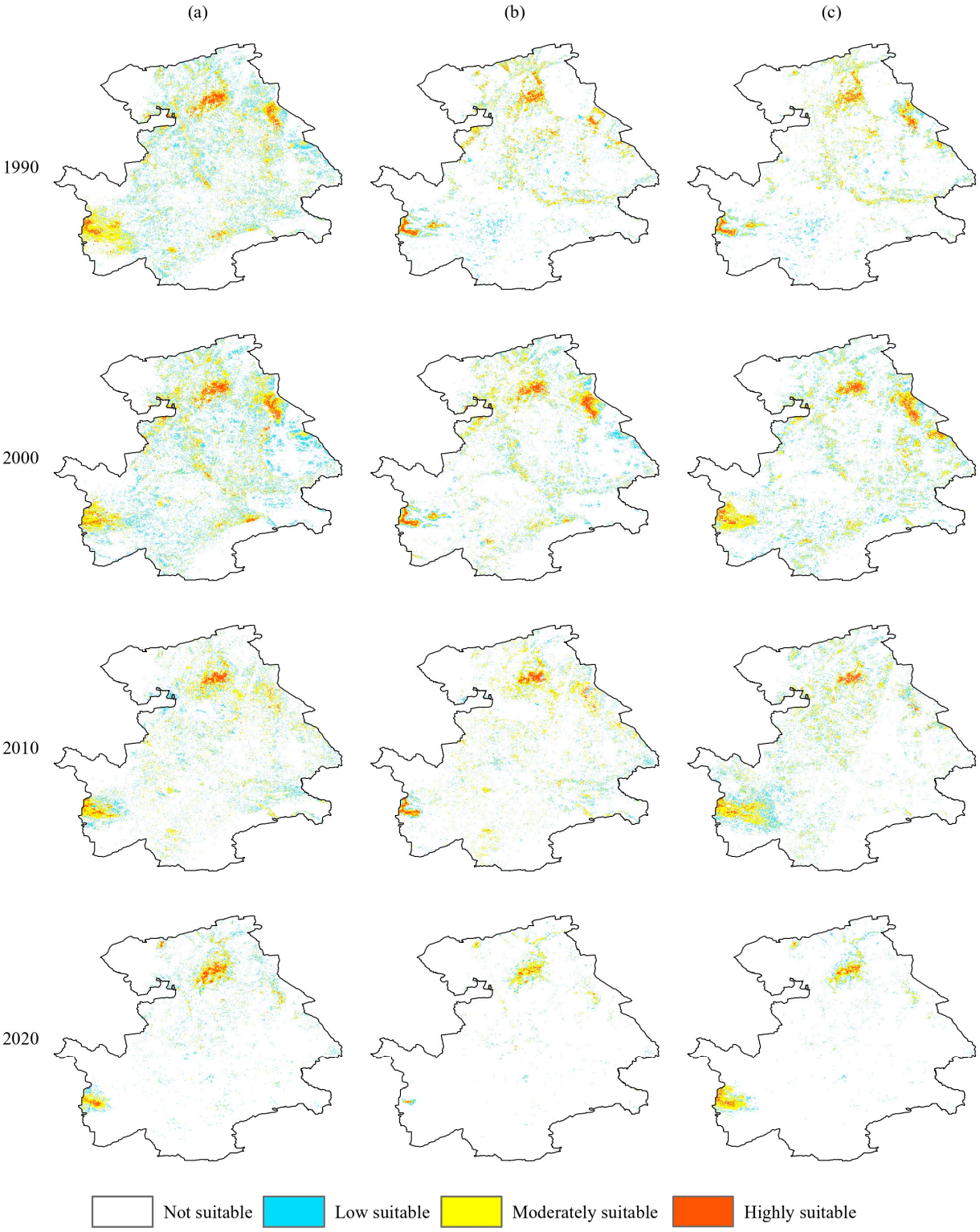


Figure 3. Spatiotemporal distribution of suitable habitats for red-crowned crane. (**a**) Spatiotemporal distribution of suitable habitats during the spring migration period. (**b**) Spatiotemporal distribution of suitable habitats during the breeding season. (**c**) Spatiotemporal distribution of suitable habitats during the autumn migration period.

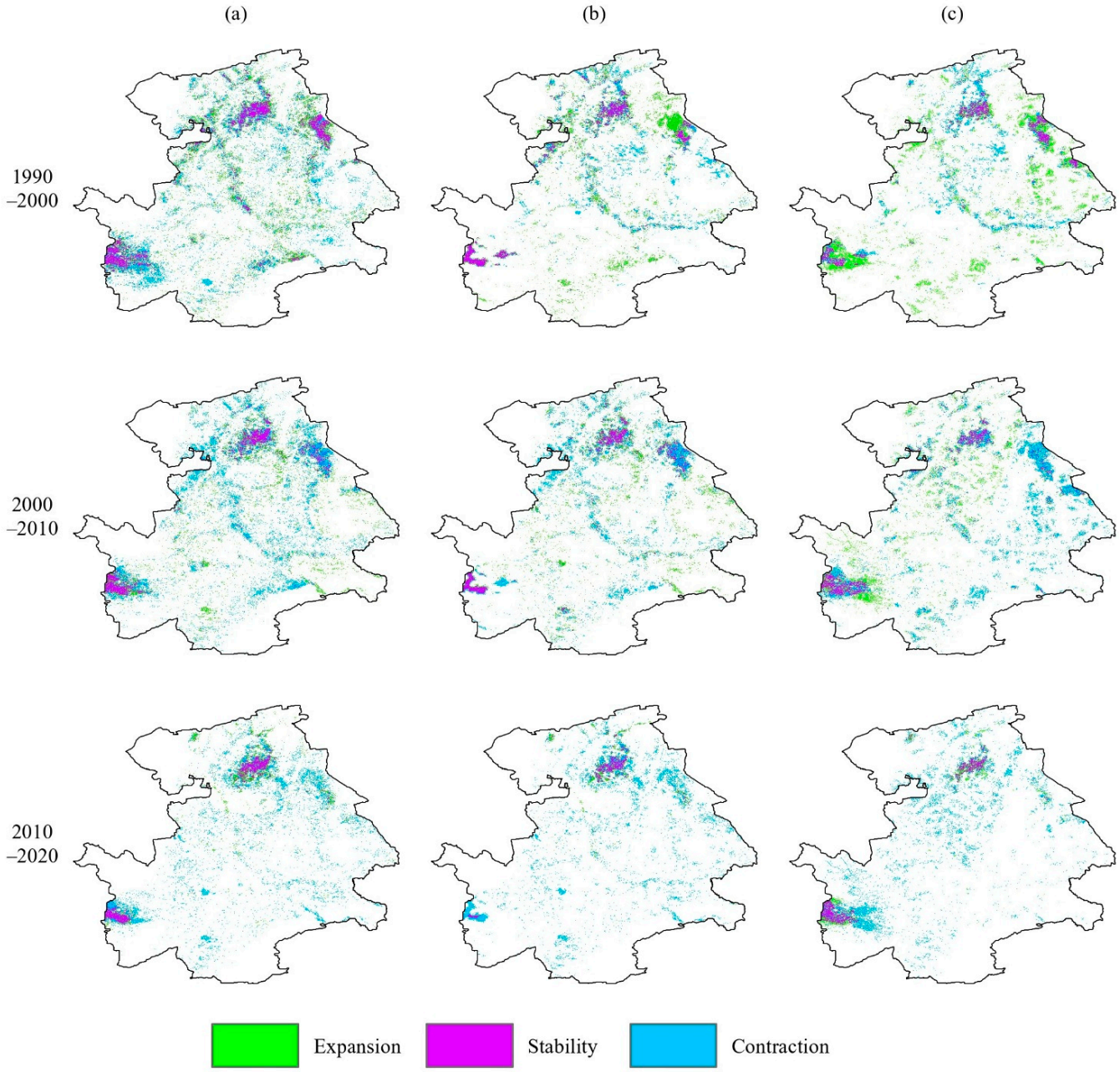


Figure 4. Spatiotemporal dynamics of suitable habitats for the red-crowned crane. (**a**) Spatiotemporal dynamics of suitable habitats during the spring migration period. (**b**) Spatiotemporal dynamics of suitable habitats during the breeding season. (**c**) Spatiotemporal dynamics of suitable habitats during the autumn migration period.

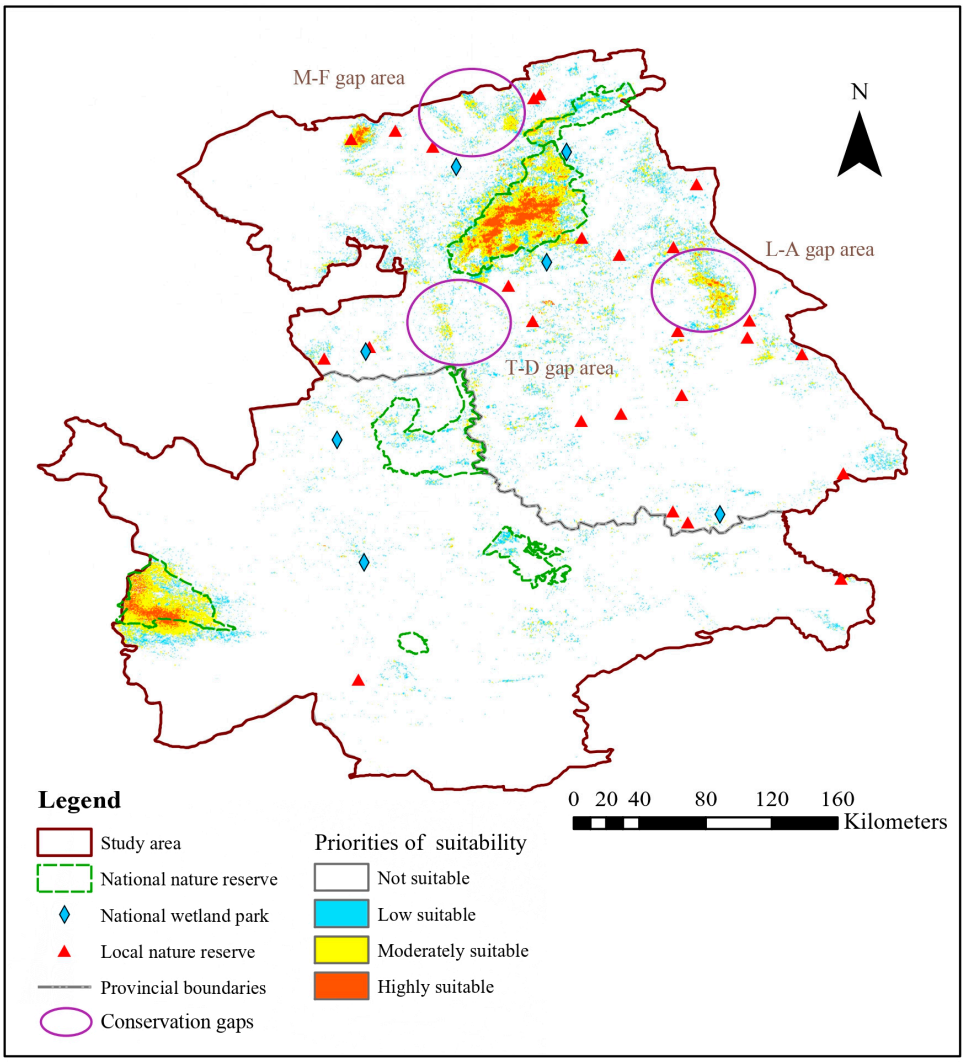


Figure 5. Conservation gaps in suitable red-crowned crane habitats on Songnen Plain. (M-F represent Meilisi Daur–Fuyu, L-A represent Lindian–Anda, and T-D represent Tailai–Dorbod).

4. Discussion

Using MaxEnt combined with ArcGIS 10.4 for spatial analysis, this study precisely mapped the potential distribution of red-crowned cranes on the Songnen Plain, identified key environmental factors affecting habitat selection at different life stages, and tracked changes in suitable habitats and the extent of this change over time. Research shows that land use type remains the main factor influencing red-crowned crane habitat choice, with a contribution significantly surpassing other variables. This pattern aligns with earlier studies and highlights the species' strong reliance on natural wetlands [15]. Concerning road disturbance, the importance of distance from roads becomes notably greater during autumn migration; data from the Songnen Plain reveal that the likelihood of crane presence increases as distance from roads exceeds 1.3 km, emphasizing traffic disturbance as a major obstacle during migration [53]. The impact of proximity to cropland varies seasonally and annually, consistent with population dynamics studies at Yancheng, which indicate that cycles of farmland expansion and wetland restoration policies jointly influence the minimum distance cranes keep from cropland [54].

Overall, suitable habitats declined substantially, and habitat suitability showed clear changes over time and across locations in all periods; this matches previous studies [55]. Since habitat quality is essential for species survival and reproduction, evaluating its

suitability is vital for conservation [56,57]. Overlay analysis of the current protected area network with key-period suitable habitat maps identified three spatial conservation gaps, showing that the existing protected area system is incomplete and does not fully encompass the crane's critical habitats [12].

By developing habitat-based species distribution models, we demonstrate that multiple environmental factors significantly affect red-crowned crane habitat selection across various life stages. All seasonal models achieved AUC values above 0.94, confirming high predictive accuracy and reliable identification of key environmental factors. Land use was the primary predictor during spring migration, breeding, and autumn migration, reflecting the red-crowned crane's strong preference for specific habitat types such as wetlands. Wetlands and marsh meadows are essential for their survival and reproduction [55,58,59]. The significance of distance from cropland during spring and autumn migrations indicates that cranes forage in croplands, but proximity increases the risk of human disturbance [60]. Altitude also influenced habitat selection during spring migration, likely because it correlates with climate conditions and food availability [59]. The crucial role of distance from roads during autumn migration underscores how transportation infrastructure can considerably degrade habitat quality [60].

Spatially, suitable habitats for the red-crowned crane have experienced significant changes. Highly and moderately suitable patches often overlap, while areas with low suitability and those unsuitable have repeatedly alternated. This has shifted the overall distribution from a relatively continuous area to a more fragmented mosaic. However, across the Songnen Plain, the total number of breeding (about 200) and migratory (around 500) red-crowned cranes has remained stable over the past three decades, despite the area of highly suitable habitats that is actually occupied decreasing by more than half [61]. These findings indicate that the contraction in distribution is not solely due to fewer cranes but also reflects a genuine reduction in their occupied range [55]. From 1990 to 2020, the spatial extent of suitable habitats contracted sharply, so that by 2020, they was mostly confined within existing nature reserves. The decline in habitat suitability increases the challenges red-crowned cranes face in meeting basic needs such as food, breeding sites, and predator avoidance, which could directly impact their population size and viability [62]. Land use change is a major driver of this decline. Agricultural expansion, rapid urbanization, and wetland reclamation have transformed the original land cover, disrupted habitat structure and function, and decreased suitability [63,64]. Meanwhile, climate change has exerted additional pressure. Variations in temperature and rainfall affect wetland water levels and plant dynamics, further altering habitat quality [64]. Habitat fragmentation and contraction can isolate local populations, increase extinction risks, and threaten long-term survival and reproduction [62]. Therefore, protecting and restoring suitable habitats—mainly by expanding and reconnecting existing patches—is crucial for the sustainable conservation of the red-crowned crane.

Habitat suitability for red-crowned cranes during spring migration, breeding, and autumn migration shows clear spatiotemporal variation. During spring migration, suitable habitats from 1990 to 2000 were mainly located in the lower Wuyuer River basin of the Nenjiang River and in the floodplain formed by the middle and lower Nenjiang River and its tributary, the Yalu River, on the Songnen Plain. It sharply contracted from 2000 to 2010 and became more concentrated within a few nature reserves and their nearby areas from 2010 to 2020. During the breeding season, suitable habitats in 1990 were spread across the Wuyuer River basin and the lower reaches of the Taoer and Huolin Rivers on the Songnen Plain. The distribution expanded in 2000, but by 2010 to 2020, it was nearly entirely confined to breeding-site nature reserves, including Xianghai, Momoge, Halahai, and Zhalong. In autumn migration, suitable habitats from 1990 to 2000 were located in

Qiqihar and Daqing in Heilongjiang Province and in Tongyu and Taonan counties in Jilin Province. The range shrank in 2010, and by 2020, it remained only in a few areas, such as Zhalong. These spatiotemporal changes in habitat suitability reflect the combined effects of human disturbance and natural environmental shifts on red-crowned crane habitat [62,65]. Studies indicate that habitat fragmentation and declining quality pose common threats to endangered species, mainly driven by human activities and climate change [66].

Regarding the change in suitable habitats, the period from 1990 to 2010 experienced the most significant fluctuations, while from 2010 to 2020, the level of change decreased and stabilized somewhat. Over the 30 years, there were notable seasonal differences, with the largest suitable habitat during spring migration, smaller habitats during the breeding season, and the smallest habitat during autumn migration. This pattern reflects different habitat preferences at various life stages [58]. During spring migration, red-crowned cranes tolerate lower-quality reed marshes and forage easily in post-burn croplands, resulting in a large suitable area; during the breeding season, they specifically select high-quality reed marshes, leading to a much smaller suitable area; in autumn migration, reed marshes mainly become unsuitable, and pre-harvest croplands limit foraging to field edges, resulting in the smallest suitable area [58,59]. These differences highlight the species' flexible but stage-specific habitat needs, which should be carefully considered when developing conservation strategies.

The 2020 distribution map of suitable habitats for the red-crowned crane shows that the core areas are the national nature reserves of Zhalong and Wuyuer River in Heilongjiang Province, and Xianghai in Jilin Province. Geographically, the crane's current range is fragmented, with suitable habitat patches mostly separated. This fragmentation threatens population stability and growth. Therefore, we need to protect existing suitable habitats and also restore and improve the quality of marginal habitats through targeted efforts.

Although presence data limitations prevent us from reporting precise population sizes for 1990, 2000, 2010, and 2020, available evidence suggests that the total number of breeding individuals (around 200) and migratory cranes (about 500) in the Songnen Plain has remained relatively stable over the past three decades [61]. In contrast, the area of highly suitable habitats has sharply decreased. Previous studies have shown that habitat change is recognized as one of the main causes of the decline in the western population of red-crowned cranes [55]. Overall, these findings show that the contraction in distribution is not just due to fewer individuals but also reflects a genuine reduction in the range they occupy.

The results show the combined influence of the "wetland vs. non-wetland" gradient and key disturbance factors. A selected sample of wetland sites will be needed to understand why some wetlands are inhabited while others that appear similar remain unoccupied.

5. Conclusions

Based on a 30-year analysis of suitable habitats for the red-crowned crane, land use has become the primary factor in habitat selection. Meanwhile, the influence of both road distance and cropland distance has gradually decreased. Road distance now mainly serves as an avoidance factor, while cropland is increasingly recognized as a type of habitat. Overall, suitable habitats have continuously shrunk and become more fragmented. Examining changes in suitability classes indicates that suitable areas are gradually becoming unsuitable, and the spatial pattern has shifted from being relatively continuous to highly patchy. Additionally, the spatial distribution of suitable habitats has contracted to the extent that the crane has disappeared from many of its former strongholds.

A gap analysis of suitable red-crowned crane habitats within existing protected areas in the Songnen Plain identifies three conservation gaps: the Lindian–Anda, Tailai–Dorbod, and Meilisi Daur–Fuyu gaps. To enhance habitat protection for the red-crowned crane, we recommend establishing a protected area network centered on national parks, with

a specific proposal to create the "Crane Homeland National Park." This network should encompass the northern, southern, eastern, and central regions of the Songnen Plain, integrating nature reserves into a unified system. Utilizing species distribution models to identify potential habitats and monitor range shifts is crucial for effective conservation and science-based management of this endangered species.

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