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Special Issue Reprint

Conflict and Coexistence Between Humans and Wildlife

Edited by
Li Zhang

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Conflict and Coexistence Between Humans and Wildlife

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Guest Editor

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About the Editor

Li Zhang

Li Zhang is a Professor of Ecology and doctoral supervisor at Beijing Normal University. He serves on the National Endangered Species Science Committee. He is Executive Director of the China Environmental Protection Federation. He also serves as Executive Director and Deputy Director of the Conservation Biology Subcommittee of the China Zoological Society, and as Deputy Director of the Animal Ecology Committee of the Ecological Society of China. He is also a senior advisor to the UNEP Science Policy Business Forum and an Ombudsperson for the Society for Conservation Biology. His research spans human–wildlife relationships, conservation biology, ecosystem service valuation, nature reserve legislation, collective forest tenure reform, community-based conservation agreements, and policy supporting the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). He develops community-led conservation models and provides scientific evidence for wildlife legislation and trade governance. He has published over 100 peer-reviewed papers in journals including *Nature Ecology and Evolution*, *PNAS*, *Trends in Ecology and Evolution*, *Conservation Letters and Ecosystem Services*, and six World View and Correspondence pieces in *Nature* and *Science*. He previously held leadership roles at IFAW, advancing animal welfare and wildlife conservation in China, and served on Conservation International's China senior management team before becoming China Program Head, supporting field conservation and community engagement across southwest China. He organizes sessions on human–wildlife coexistence and community conservation at international conservation forums. As Vice President of the Society of Entrepreneurs and Ecology and Vice Chair of the SEE Foundation, he promotes wildlife conservation and collaboration among diverse stakeholders across China.

Preface

This Reprint compiles interdisciplinary studies focusing on human–wildlife conflict and coexistence amid global ecological and socioeconomic changes. It aims to rethink traditional wildlife conservation paradigms by shifting from passive conflict mitigation to sustainable human–nature coexistence governance. The collected works cover field observations, spatial–temporal behavioral analyses of wild ungulates, livestock disturbance effects, socioecological driving mechanisms, and community-based conservation strategies. Targeting ecologists, conservation practitioners, and environmental policymakers, this Reprint provides empirical evidence and practical references for balancing biodiversity protection with local livelihood demands, helping advance context-adaptive, equitable, and long-term human–wildlife coexistence management worldwide.

Li Zhang
Guest Editor

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Editorial

From Conflict to Coexistence: Rethinking Human-Wildlife Relationships in a Changing World

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1. Introduction

Human–wildlife interactions have become one of the most pressing challenges in contemporary biodiversity conservation. As human populations expand and land-use change intensifies, encounters between people and wildlife are increasing in both frequency and complexity. These interactions often manifest as conflict, including crop damage, livestock depredation, property loss, and risks to human safety. At the same time, wildlife populations are subjected to mounting pressures from habitat fragmentation, resource competition, and direct persecution [1,2]. The dual imperatives of safeguarding biodiversity and ensuring human well-being place human–wildlife conflict at the center of conservation science and policy.

In recent years, the conceptual framing of these interactions has shifted from a narrow focus on conflict toward a broader understanding of coexistence. Coexistence emphasizes the dynamic and context-dependent relationships between humans and wildlife, recognizing that interactions are shaped not only by ecological conditions but also by social, economic, and institutional factors [3,4]. This Special Issue in *Diversity* seeks to advance this perspective by bringing together interdisciplinary contributions that examine both the drivers of conflict and the pathways toward sustainable coexistence.

2. Ecological and Socioeconomic Drivers of Conflict

Human–wildlife conflict is fundamentally rooted in ecological processes that are increasingly influenced by anthropogenic change. Habitat loss and fragmentation alter species distributions and movement patterns, often forcing wildlife into closer proximity with human-dominated landscapes [5,6]. In parallel, climate change and environmental variability can modify resource availability, intensifying competition for food, water, and space, thereby amplifying conflict risks globally [7,8]. These ecological dynamics are further complicated by species-specific behavioral adaptations, including changes in foraging strategies and activity patterns in response to human presence [9].

However, conflict cannot be fully understood through ecological mechanisms alone. Socioeconomic conditions play a critical role in shaping both the occurrence and perception of human–wildlife interactions. Livelihood's dependence on natural resources, levels of economic vulnerability, and access to institutional support all influence how communities experience and respond to wildlife-related risks [10,11]. In many contexts, conflict is exacerbated not simply by the magnitude of damage but by inequities in its distribution and the perceived fairness of mitigation and compensation mechanisms [12]. As such, human–wildlife conflict represents a coupled socio-ecological phenomenon that requires integrated analytical approaches.

3. From Conflict Mitigation to Coexistence Frameworks

Traditional approaches to managing human–wildlife conflict have largely focused on reactive mitigation strategies, including physical barriers, deterrents, and compensation schemes. While these measures can reduce immediate losses, their effectiveness is often limited by issues of scalability, sustainability, and social acceptance [13,14]. Increasingly, attention has shifted toward proactive and systemic approaches that aim to enable long-term coexistence.

Coexistence frameworks emphasize the importance of aligning ecological objectives with human needs and values. This involves not only reducing the negative impacts of wildlife but also enhancing the conditions under which humans and wildlife can share landscapes [3,15]. Key elements include adaptive land-use planning, community engagement, and the incorporation of local knowledge into conservation strategies [16]. Moreover, coexistence requires institutional arrangements that support equitable benefit-sharing and conflict resolution, as well as governance structures capable of responding to dynamic environmental and social conditions [17].

Recent advances in spatial modeling and risk assessment have further contributed to this transition by enabling the identification of conflict hotspots and the design of targeted interventions [18,19]. These tools allow for a more nuanced understanding of where and when conflicts are likely to occur, thereby facilitating more efficient allocation of resources and more effective policy implementation.

4. Institutional and Policy Dimensions

The governance of human–wildlife interactions is a critical determinant of conservation outcomes. Effective policy frameworks must balance ecological protection with social equity, ensuring that the costs and benefits of conservation are distributed fairly among stakeholders [20,21]. In many regions, compensation and insurance mechanisms have been introduced to offset economic losses associated with wildlife damage. While these systems can alleviate immediate burdens, their long-term effectiveness depends on accurate damage assessment, timely compensation, and sustainable funding sources [22,23].

Beyond compensation, there is growing recognition of the need for multi-stakeholder approaches that involve governments, local communities, private sectors, and civil society organizations [24]. Such approaches can enhance legitimacy and foster collective action, particularly in contexts where conservation objectives intersect with local livelihoods [25]. In addition, the integration of technological innovations, including real-time monitoring systems and data-driven decision-making tools, offers new opportunities to improve transparency and efficiency in governance [26].

Importantly, policy interventions must be sensitive to cultural and social contexts. Attitudes toward wildlife are shaped by historical experiences, belief systems, and social norms, all of which influence the acceptability of different management strategies [27]. Understanding these dimensions is essential for designing interventions that are not only effective but also socially sustainable.

5. Contributions of This Special Issue

The articles included in this Special Issue reflect the diversity and complexity of human–wildlife interactions across different ecological and geographic contexts. They encompass a range of methodological approaches, from empirical field studies and spatial modeling to policy analysis and interdisciplinary synthesis. Collectively, these contributions highlight the importance of integrating ecological data with social and institutional perspectives in order to develop comprehensive solutions to human–wildlife conflict.

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Several studies focus on the ecological underpinnings of conflict, examining species distribution, habitat use, and behavioral responses to environmental change. Others explore the socioeconomic and governance dimensions, including compensation mechanisms, community-based management, and policy innovation. Together, these works contribute to a more holistic understanding of coexistence, emphasizing the need for cross-scale and cross-sectoral approaches.

6. Future Directions

Advancing the science and practice of human–wildlife coexistence requires continued efforts to bridge disciplinary boundaries and to translate research into actionable policy. Future research should prioritize the integration of ecological and social data, the development of scalable and context-sensitive interventions, and the evaluation of long-term outcomes. In particular, there is a need to better understand how behavioral, institutional, and technological innovations can interact to support sustainable coexistence [3,28].

At the same time, global environmental change will continue to reshape the conditions under which humans and wildlife interact. Addressing these challenges will require adaptive and forward-looking strategies that can accommodate uncertainty and complexity. By fostering collaboration among researchers, practitioners, and policymakers, the field can move toward more effective and equitable conservation outcomes.

7. Concluding Remarks

Human–wildlife conflict represents not only a challenge but also an opportunity to rethink the relationship between humans and nature. Moving beyond conflict toward coexistence entails recognizing the interconnectedness of ecological and social systems and embracing approaches that are both scientifically robust and socially inclusive. This Special Issue aims to contribute to this ongoing transformation by providing new insights and perspectives on one of the most critical issues in biodiversity conservation today.

Conflicts of Interest: The authors declare no conflict of interest.

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Article

The Impact of Livestock on the Spatiotemporal Activity of Ungulates in Western Sichuan, China

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Abstract

Grazing is a widespread land use practice with significant implications for biodiversity and ecosystem functioning. Wild ungulates, as key components of terrestrial ecosystems, play a vital role in maintaining ecosystem health. Dietary overlap exposes wild ungulates to intense competition with livestock, yet the effects of grazing on them remain underexplored. Using camera-trapping data from Xinglong County in the mountains of Southeast China, we investigated the spatiotemporal responses of eight wild ungulates to livestock (cattle and horses). Our results showed the following: (1) The potential distribution of suitable habitats for ungulates was primarily shaped by elevation (ELE), distance to temple (DTT), precipitation of the coldest quarter (bio19), and distance to water (DTW). Among the species, blue sheep (*Pseudois nayaur*) showed the strongest response to livestock presence. (2) Spatially, most ungulates appeared to avoid livestock; forest musk deer (*Moschus berezovskii*) showed spatial avoidance of horses. (3) Temporally, the daily activity patterns of most ungulates generally showed low to moderate overlap with those of cattle. These findings suggest that livestock grazing may be associated with negative effects on wild ungulates in Xinlong County. Given the ecological importance of ungulates, the need to maintain wildlife community integrity, and the long history of grazing in the region, further research is warranted to understand the role of livestock in shaping wildlife communities.

Keywords: suitable habitat; spatial interaction; daily activity rhythm; grazing; mountains of southwest China

1. Introduction

The overexploitation of natural resources by humans has led to a rapid decline in species and natural habitats, making biodiversity conservation an urgent priority [1–3]. To mitigate the loss of biodiversity, government authorities and related agencies have implemented various measures, such as establishing protected areas [4], imposing restrictions on deforestation [5], and enforcing severe penalties for poaching [6]. These efforts have helped reduce the impact of human disturbance on wildlife to some extent [7].

However, as deforestation and poaching have been reduced, grazing has emerged as another activity significantly impacting wildlife, drawing the attention of scholars. Studies have shown that as the human population increases, so does the demand for livestock [8]. Currently, livestock production occupies more than a quarter of the global land surface area [9], making it one of the most extensive land uses and having a significant impact on

plant and animal communities and ecosystems [10]. High-intensity grazing can significantly reduce plant biomass in the understory shrub layer, thus affecting herbivore activities [6]. A study on the giant panda (*Ailuropoda melanoleuca*) found that free-range livestock can significantly negatively impact bamboo biomass and regeneration [11]. Furthermore, grazing activities also affect carnivore competition [12]. High-density livestock activities lead to the decline of wildlife resources and habitat loss, intensifying spatial competition between tigers (*Panthera tigris*) and leopards (*Panthera pardus*), and even resulting in the disappearance of local populations [13,14].

Wild ungulates are an essential component of terrestrial ecosystems, influencing the composition and function of vegetation and soil communities [15–17] and providing an energy source for predators [18]. Ungulates affect ecosystems through browsing, trampling, defecation, and seed dispersal [19,20]. For carnivores, especially apex predators, the abundance of ungulates largely determines the possibility of multiple predators coexisting [21,22]. Studies have shown that grazing can significantly affect the activity of wild ungulates and their habitat quality [23] and lead to population decline [24]. Free-range livestock may compete with wild animals for food resources and living space, crowding them out to a certain extent [23,25]. However, some studies have found that grazing does not have an entirely negative effect on ungulates [26]. Therefore, given the importance of ungulates and the potential impact of grazing activities on them, it is worth further exploring the relationship between the two parties.

The mountains of southwest China are recognized globally as a biodiversity hotspot, harboring a variety of wild ungulates [27,28]. With the implementation of the Natural Forest Protection Project and the Grain for Green Project, human disturbances such as forest logging in this area have been effectively controlled. However, the long history of grazing has become one of the main factors affecting wildlife. Despite this, few studies have reported the effects of grazing on sympatric wild ungulates [29,30].

Xinlong County, located in the mountains of southwest China, is home to a variety of carnivores and ungulates [31] and is also a traditional Tibetan gathering area [32]. Livestock is the main source of income for local villagers. Existing studies have found that human presence has little impact on ungulates, with most ungulates coexisting spatially with humans [32]. However, the effects of grazing on the distribution of wild ungulates in this area have not been reported. Grazing activities are one of the most significant anthropogenic disturbances in the mountains of southwest China. Xinlong, with its long history of grazing and as one of the few areas in this region that still harbors intact wildlife communities, presents a valuable opportunity to study ungulates. Focusing on the ungulates in Xinlong can deepen our understanding of the impact of grazing on these species and provide a unique case study for the conservation of ungulate populations in the mountains of southwest China. Based on this, our study focuses on Xinlong, using various ungulates as research subjects to explore the effects of grazing on their temporal and spatial activities. The goal is to clarify the potential impacts of grazing activities on these ungulate species. We anticipate that grazing activities may influence the spatiotemporal patterns of ungulates.

Xinlong County, a traditional pastoral area with an intact wildlife community, provides a unique opportunity to investigate livestock–wildlife interactions in the mountains of southwest China. Despite this, quantitative assessments of how livestock affect sympatric wild ungulates in this region remain scarce. To address this gap, we used two years of camera-trap data to: (1) assess the influence of livestock (cattle and horses) on the spatial distribution and habitat suitability of eight ungulate species; (2) test whether ungulates exhibit spatial or temporal avoidance of livestock; and (3) quantify the extent of diel activity overlap between ungulates and livestock. By clarifying these responses, our study

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aims to provide empirical evidence for managing livestock–wildlife coexistence in alpine ecosystems of the Qinghai–Tibet Plateau.

2. Materials and Methods

2.1. Study Area

Xinlong lies on the eastern edge of the Qinghai–Tibet Plateau, where the western Sichuan Plateau meets the Hengduan Mountains (99°37′–100°54′ E, 30°23′–31°32′ N, Figure 1). The Yalong River flows through the area from north to south, carving a rugged landscape of mountains and canyons with an elevation range exceeding 3000 m. The climate is subtropical humid monsoon, with cold, dry winters and warm, rainy summers. This topography and climate create a diverse array of habitats, supporting one of the most intact and biodiverse ecosystems in China. At least 11 ungulate species (Table 1), including white-lipped deer (*Przewalskium albirostris*), red deer (*Cervus elaphus*), sambar deer (*Rusa unicolor*), Chinese serow (*Capricornis milneedwardsii*), Chinese goral (*Naemorhedus griseus*), blue sheep (*Pseudois nayaur*), forest musk deer (*Moschus berezovskii*) and alpine musk deer (*Moschus chrysogaster*), inhabit this region [31]. Additionally, the area supports at least six large carnivore species, including leopards (*Panthera pardus*), snow leopards (*P. uncia*), Eurasian lynx (*Lynx lynx*), wolves (*Canis lupus*), brown bears (*Ursus arctos*), and Asiatic black bears (*U. thibetanus*).

Table 1. List of ungulate species recorded by camera traps in Xinlong, China, from 2022 to 2023.

Family	Species	Latin Name	National Protected Category	IUCN Red List	No. of Grids	No. of Independent Photos	Relative Abundance Index
Bovidae	Chinese goral	*Naemorhedus griseus*	II	-	60	378	5.11
	Chinese serow	*Capricornis milneedwardsii*	II	VU	173	1483	20.06
	blue sheep	*Pseudois nayaur*	II	LC	17	579	7.83
Cervidae	white-lipped deer	*Przewalskium albirostris*	I	VU	15	37	0.5
	red deer *	*Cervus elaphu*	I	LC	1	2	0.03
	tufted deer	*Elaphodus cephalophus*	II	NT	120	1889	25.55
	sambar deer	*Rusa unicolor*	II	VU	108	1357	18.35
	Siberian roe deer	*Capreolus pygargus*	-	LC	8	39	0.53
Moschidae	forest musk deer	*Moschus berezovskii*	I	EN	82	1055	14.27
	alpine musk deer	*M. chrysogaster*	I	EN	99	788	10.66
Suidae	wild boar	*Sus scrofa*	-	LC	158	985	13.32

*: Red deer were recorded only once; thus, they were not included in subsequent analyses.

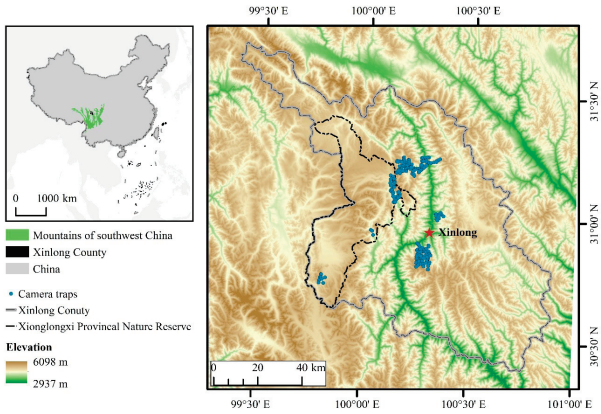

Figure 1. Distribution of 2022–2023 camera trap locations in Xinlong, China.

2.2. Data Collection

2.2.1. Camera Trapping Surveys

Between March 2022 and November 2023, we set up more than 240 infrared camera traps across Xinlong following a 1 km × 1 km grid. After accounting for equipment loss, 226 traps provided usable data. Each unit was mounted 0.4–0.6 m above ground on a tree trunk or similar stable structure, set to operate 24 h/day with medium sensitivity, and programmed to record three photographs and a 20-s video per trigger event, with a 1-min interval between triggers. To ensure spatial independence, cameras were placed more than 500 m apart. Sites were selected in areas with signs of wildlife activity (e.g., near water sources, animal trails, or direct signs such as tracks or scat). The elevation of camera locations ranged from 3000 to 5000 m, covering a range of vegetation types.

We defined all photos or videos of the same species taken within a 30-min time frame as a single independent photo [28]. A single camera operating continuously for 24 h is defined as one camera day. The effective number of camera days for each camera is determined by the time interval between the first and last photos captured by that camera. This was used as the basis to calculate the relative abundance index (RAI). The RAI serves as an indicator for assessing the relative population size of species. The index was calculated using the following formula [33]:

$$\text{RAI} = (\text{independent photos}/\text{total camera days}) \times 1000$$

2.2.2. Species Distribution Data

To increase the number of occurrence records for the species distribution models, we combined the 2022–2023 grid-based camera data with earlier surveys (2015–2021) that used a random sampling design [32]. For each species, we compiled presence records from both periods. Locations where a camera operated for one year or more without recording the target species were treated as absence points. To reduce spatial autocorrelation, we applied a filtering procedure: presence points were buffered by 1 km, and any absence point falling within this buffer was discarded. A second 1 km filter was then applied to both presence and absence points to ensure that no two points (regardless of type) were closer than 1 km. These procedures were implemented in ArcGIS 10.8 (https://support.esri.com/, accessed on 8 April 2026).

2.2.3. Environment Variables

Based on relevant research, this study selected four environmental factors to include models of ungulates, including topography, bioclimate, vegetation, and disturbance (Table 2). The topographic factors included elevation (ELE), aspect (ASP), slope (SLP), terrain roughness index (TRI), and distance to water (DTW) [23]. These variables were extracted from DEM and calculated using ArcGIS 10.8 (https://support.esri.com/). Bioclimate factors included 14 variables, such as bio10 (mean temperature of the warmest quarter), bio18 (precipitation of the warmest quarter), and bio19 (precipitation of the coldest quarter), all of which were sourced from Worldclim (https://worldclim.org/) [34]. Vegetation factors were represented by the enhanced vegetation index (EVI). We divided EVI into two types: EVI_W, indicating the average index for the warm season months, and EVI, representing the annual average vegetation index. EVI_W was obtained by downloading monthly satellite images from Landsat 8 (May to October) via the Geospatial Data Cloud (https://www.gscloud.cn/). These images were processed using ENVI 5.3 for atmospheric correction and radiometric calibration, followed by the calculation of the vegetation index using the vegetation index calculation tool. EVI obtained from the National Tibetan Plateau Data Center (https://data.tpdc.ac.cn/) [35]. Disturbance covariates comprised distance to

road (DTD), distance to settlement (DTS), distance to temple (DTT), and livestock activity probability (Ls). Distance to temple serves as a proxy for human activity intensity, as temples in this region are often associated with villages, livestock grazing, and cultural practices that shape land use. Temple coordinates were provided by the Xinlong Forestry and Grassland Bureau; road and settlement data were obtained from the National Catalogue Service for Geographic Information (https://www.webmap.cn/). All distances were computed with the Euclidean Distance tool in ArcGIS 10.8. To obtain Ls, we used relevant methods to construct activity probability maps for cattle (represents domestic yak) and horses based on the infrared camera records of their activity sites, ultimately calculating Ls [36]. The Ls was calculated using the following formula:

$$\mathrm{Ls} = 1 - (1 - P_{cattle}) \times (1 - P_{horse})$$

where Ls is the probability of at least one livestock species was present; P is the presence probability estimated from ensemble species distribution models.

Table 2. Description of environmental variables for the analysis in Xinglong.

Variables	Codes	Data Resource	Variables Types	Analysis
Topographic factors				
Elevation (m)	ELE	https://www.gscloud.cn/	Continuous	Ensemble Occupancy
Slope (°)	SLP	Extracted from DEM	Continuous	Occupancy
Aspect	ASP	Extracted from DEM	Categorical	Occupancy
Terrain roughness index	TRI	Extracted from DEM	Continuous	Ensemble
Distance to water (m)	DTW	Extracted from DEM	Continuous	Ensemble Occupancy
Bioclimate factors				
mean temperature of the warmest quarter (°C)	bio10	https://worldclim.org/	Continuous	Occupancy
precipitation of the warmest quarter (mm)	bio18	https://worldclim.org/	Continuous	Ensemble Occupancy
precipitation of the coldest quarter (mm)	bio19	https://worldclim.org/	Continuous	Ensemble
Vegetation factors				
Annual average enhanced vegetation index	EVI	https://data.tpdc.ac.cn/	Continuous	Ensemble
Warm season average enhanced vegetation index	EVI_W	https://www.gscloud.cn/	Continuous	Occupancy
Disturbance factors				
Distance to road (m)	DTD	https://www.webmap.cn/	Continuous	Ensemble Occupancy
Distance to temple (m)	DTT	Xinlong Forestry and Grassland Bureau	Continuous	Ensemble Occupancy
Distance to settlement (m)	DTS	https://www.webmap.cn/	Continuous	Ensemble Occupancy
Livestock activity probability	Ls		Continuous	Ensemble
Other factors				
Year	Year	-	Categorical	Occupancy
Camera working days	effort	-	Continuous	Occupancy

Before model construction, we used Spearman correlation analysis to examine the correlations between all variables (Table S1). When the correlation coefficient $|r| > 0.7$ for two variables, we excluded models that included both variables (for the occupancy model) or excluded one of the variables (for the ensemble model) (Table 2).

2.3. Data Analysis

2.3.1. Ensemble Species Distribution Models

We employed ensemble species distribution models (ESDMs) to predict the potential distribution of each ungulate species [32]. These models improve predictive reliability by combining multiple algorithms [37,38]; our ESDM integrated six algorithms: generalized linear model (GLM) [39], generalized additive model (GAM) [40], generalized boosted regression model (GBM) [41], classification tree analysis (CTA) [42], random forest (RF) [43], and maximum entropy model (MaxEnt) [44].

Model validation was performed using 10-fold cross-validation, with 70% of the data used for training and 30% for testing. Predictive accuracy was assessed using the area under the receiver operating characteristic curve (AUC) [45], which is robust to occurrence frequency and threshold choice. AUC values were interpreted as follows: excellent (0.9–1.0), very good (0.8–0.9), good (0.7–0.8), fair (0.6–0.7), and poor (<0.6). Only models with AUC > 0.70 were retained.

For each species, the threshold maximizing the sum of sensitivity and specificity (MSS) [46], was used to classify presence and absence. Variable importance was expressed as a percentage contribution, and the final ensemble predictions were derived as weighted averages (weight = $(AUC - 0.5)^2$). Analyses were carried out using the SSDM package [47] in R 4.3.2 [48].

2.3.2. Two-Species Occupancy Modeling

A conditional two-species occupancy model was used to explore spatial relationships between livestock and wild ungulates [49]. Because livestock activity is highest during the warm season (May–October), we restricted our analysis to data from this period to satisfy the model's closure assumption [50] and to capture the peak period of grazing disturbance. To enhance model fit and reliability, camera sites were filtered: when two cameras were <500 m apart, the site with lower detection frequency was excluded. After this filtering, detection histories were built using 7-day sampling occasions, yielding 26 occasions; sites with <10 occasions (i.e., <70 d) were removed. The final dataset comprised 261 sites (164 from 2022 and 97 from 2023).

We first constructed single-species occupancy models for each species to select covariates for the two-species models. Covariates from the best single-species model were used as the selected covariates in the two-species analysis [49]. In addition to the environmental variables listed in Table 2, we included Year as an occupancy covariate. For detection probability, camera working days (Effort) and Year were included as detection covariates [51]. Following the assumptions of the conditional two-species occupancy model [49], we designated livestock as the dominant species (A) and ungultes as the subordinate species (B), taking into account species-specific competitive abilities. To ensure model convergence, we assumed no effect of dominant-species detection on subordinate detection (rBA = rBa).

Based on previous studies [52], we constructed eight candidate models for each species (Table S2) and ranked them by AIC. The model with the lowest ΔAIC was selected for parameter extraction and estimation of the species interaction factor (SIF) [49]. SIF = 1 indicates spatial independence; SIF < 1 indicates spatial segregation (less co-occurrence than expected by chance); SIF > 1 indicates spatial attraction (more co-occurrence than expected by chance). Models were implemented in PRESENCE 2.13.14 [53], while single-species occupancy models were fitting using the unmarked package in R 4.3.2 [48].

2.3.3. Diurnal Activity Rhythm Overlap

We assessed the diurnal activity rhythm overlap between ungulate and livestock in different regions with the coefficient of overlap [54]. The overlap coefficient (Δ) ranges from 0

to 1, with values closer to 1 indicating higher overlap, and values closer to 0 indicating lower overlap [32]. When $\Delta < 0.5$, it signifies low overlap, and when $0.5 \leq \Delta < 0.7$, it indicates moderate overlap. High overlap is denoted when $\Delta \geq 0.7$. All analyses were performed in R 4.2.3. Specifically, we used the overlap package for kernel density estimation and overlap coefficient calculations. According to the overlap coefficient results, Δ_4 provided the best predictions when the smaller sample size of the species was greater than 50; otherwise, Δ_1 was chosen [55]. Confidence intervals for the overlap coefficients were calculated using smoothed bootstrap sampling with 10,000 iterations.

3. Results

From 2022 to 2023, a total of 73,942 camera days were completed by the infrared cameras. We recorded 11 wild ungulates (Table 1), including Chinese serow (RAI = 20.06), Chinese goral (RAI = 5.11), blue sheep (RAI = 7.83), white-lipped deer (RAI = 0.50), red deer (RAI = 0.03), tufted deer (*Elaphodus cephalophus*, RAI = 25.55), sambar deer (RAI = 18.35), Siberian roe deer (*Capreolus pygargus*, RAI = 0.53), forest musk deer (RAI = 14.27), alpine musk deer (RAI = 10.66), and wild boar (*Sus scrofa*, RAI = 13.32). Based on their relative abundance indices, we selected eight species—Chinese serow, Chinese goral, blue sheep, sambar deer, tufted deer, forest musk deer, alpine musk deer, and wild boar—for further analysis.

3.1. Potential Habitat Distribution

According to the ensemble models results, all ungulate received good or higher evaluations (Chinese serow: 0.75, blue sheep: 0.82, Chinese goral: 0.82, tufted deer: 0.85, sambar deer: 0.86, forest musk deer: 0.76, alpine musk deer: 0.733, wild boar: 0.772). This indicated that the models' predictions were reliable and could effectively reflect the potential suitable habitat distribution for ungulate species in Xinlong. Here, it represents the predicted probability of species occurrence, with higher values indicating greater habitat suitability. The results showed that the potential suitable habitat area for blue sheep was 5268.20 km^2, primarily distributed in high-altitude regions. For the Chinese serow, it was 3824.22 km^2; for sambar deer, 2914.46 km^2; for Chinese goral, 2087.44 km^2; for tufted deer, 3420.20 km^2; for forest musk deer, 3576.01 km^2; and for alpine musk deer, 3324.60 km^2, all mainly distributed in the understory areas along both sides of the Yalong River. The wild boar's potential suitable habitat area was 4706.31 km^2, distributed throughout most of the county (Figure 2). These patterns reflect the distinct habitat preferences of different ungulate species, with some favoring high-altitude grasslands (e.g., blue sheep) and others favoring forested areas along the Yalong River (e.g., forest musk deer).

The results of the importance of environmental variables indicated that elevation (ELE), distance to temple (DTT), precipitation of the coldest quarter (bio19), and distance to settlement (DTS) were the primary factors influencing the potential suitable habitat distribution of ungulates, with average importance values of 15.53%, 12.08%, 11.95%, and 10.81%, respectively (>10%) (Table S3). Specifically, the potential suitable habitat distribution for the Chinese serow was mainly influenced by bio19 (17.77%), DTS (17.13%), and the enhanced vegetation index (EVI, 11.74%). The sambar deer's habitat was primarily influenced by ELE (28.35%), DTT (20.09%), and DTS (15.21%). The blue sheep's distribution was mostly affected by DTT (22.54%), livestock activity probability (Ls, 19.35%), precipitation of the warmest quarter (bio18, 14.47%), and bio19 (11.54%). The Chinese goral's habitat was influenced mainly by ELE (21.73%), EVI (15.39%), bio18 (13.57%), and bio19 (11.33%). The tufted deer's distribution was primarily affected by ELE (27.24%), distance to water (DTW, 11.27%), bio19 (11.24%), and terrain ruggedness index (TRI) (10.66%). The forest musk deer's habitat was mainly influenced by bio19 (17.33%), DTT (14.09%), ELE (13.14%),

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and DTS (11.59%). The alpine musk deer and wild boar showed more evenly distributed influence from various environmental variables (Table S3).

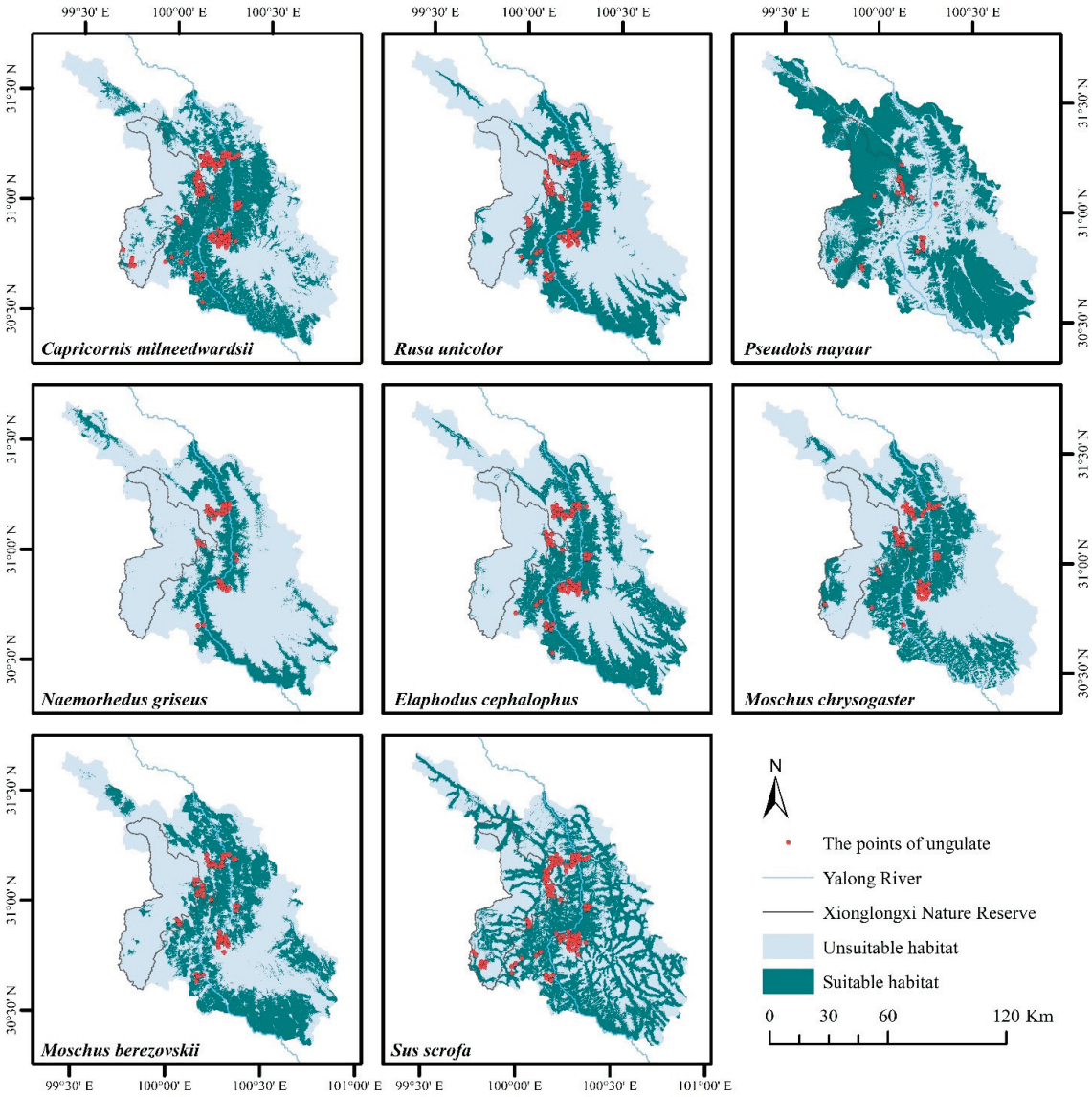

Figure 2. Potential suitable habitat distribution of wild ungulates in Xinglong. The species shown are Chinese serow (*Capricornis milneedwardsii*), sambar deer (*Rusa unicolor*), blue sheep (*Pseudois nayaur*), Chinese goral (*Naemorhedus griseus*), tufted deer (*Elaphodus cephalophus*), alpine musk deer (*Moschus. chrysogaster*), forest musk deer (*Moschus berezovskii*), and wild boar (*Sus scrofa*).

According to the environmental response curves, the habitat suitability index for blue sheep decreased with increasing livestock activity probability, while the habitat suitability index for the other ungulates increased with increasing activity probability (Figure 3). Additionally, we found that the habitat suitability index for most ungulate species decreased as DTT and DTS increased (Figure S1). Notably, blue sheep exhibited the highest habitat suitability index at distances of 10–20 km from temples, whereas forest musk deer showed the lowest suitability within this range (Figure S1).

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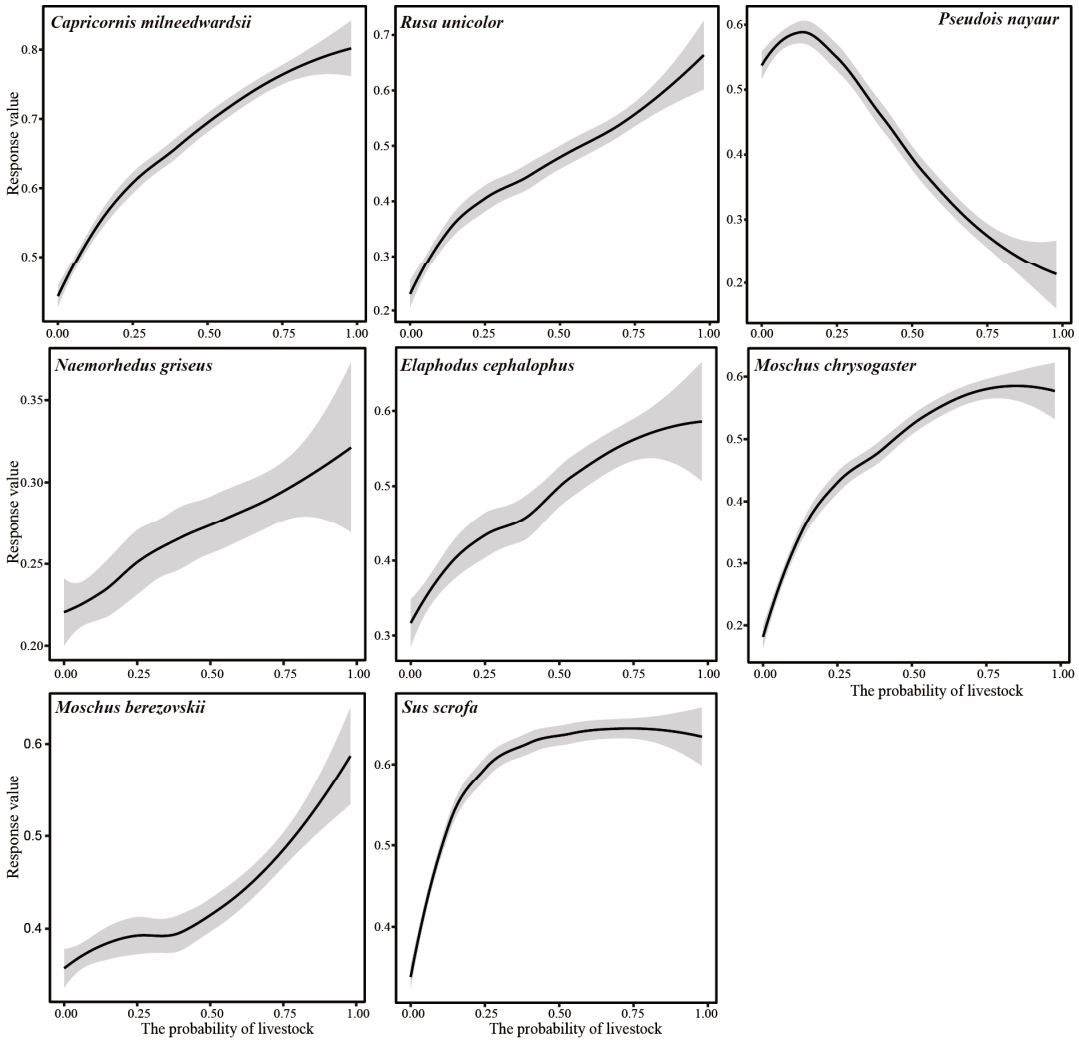

Figure 3. Response of potential suitable habitat distribution of different ungulates to livestock activity probability. The species shown are Chinese serow (*Capricornis milneedwardsii*), sambar deer (*Rusa unicolor*), blue sheep (*Pseudois nayaur*), Chinese goral (*Naemorhedus griseus*), tufted deer (*Elaphodus cephalophus*), alpine musk deer (*Moschus. chrysogaster*), forest musk deer (*Moschus berezovskii*), wild boar (*Sus scrofa*).

3.2. Spatial Interaction

Based on the results of the optimal model from the single-species occupancy models, we identified the environmental variables to be included in the two-species occupancy model analysis. Details are provided in Table 3 and Table S4.

Table 3. The optimal model results of covariates choosing for species by using single-species occupancy models.

Species	Optimal Model	N	AIC	AIC Weight	Occupancy Rate
Chinese goral	*p*(.), *psi*(EVI_W + ELE + DTT)	5	1278.26	0.02	0.24
Forest musk deer	*p*(Year), *psi*(Year + EVI_W + DTT + DTW)	7	1527.42	0.03	0.26
Tufted deer	*p*(effort + Year), *psi*(ASP + DTT + bio18)	9	3423.03	0.04	0.49
Alpine musk deer	*p*(effort), *psi*(EVI_W + DTT + DTW)	6	1763.65	0.02	0.36
Chinese serow	*p*(effort + Year), *psi*(ELE + DTD)	6	3829.89	0.06	0.71
Sambar deer	*p*(effort), *psi*(Year + ELE + DTT)	6	2313.23	0.03	0.37
Wild boar	*p*(effort), *psi*(Year + EVI_W + bio18)	6	2396.58	0.03	0.53
Blue sheep	*p*(.), *psi*(Year + EVI_W + ELE + DTT + DTW + DTD)	8	478.15	0.02	0.06
Cattle	*p*(Year), *psi*(Year + ASP + EVI_W + DTT + SLP + bio10)	11	4887.91	0.03	0.72
Horse	*p*(effort + Year), *psi*(ASP + EVI_W + ELE + DTD)	10	557.38	0.01	0.10

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The results of the two-species occupancy models indicated that: (1) Apart from wild boar, which showed a spatial preference for co-occurrence with cattle (SIF = 1.08 ± 0.00), all other ungulates remained independent of cattle (SIF = 1.00 ± 0.00); (2) Blue sheep (SIF = 2.84 ± 0.46) and Chinese serow (SIF = 1.04 ± 0.01) exhibited a spatial preference for co-occurrence with horses; (3) forest musk deer showed a spatial preference for avoiding horses (SIF = 0.95 ± 0.02); and (4) wild boar, alpine musk deer, tufted deer (SIF = 1.00 ± 0.01), sambar deer, and Chinese goral all preferred to remain independent of horses (SIF = 1.00 ± 0.00). The specific results of the two-species occupancy models are provided in Table S5.

3.3. Differences in Daily Activity Rhythms

Results showed that livestock (cattle and horses) were active primarily during the warm season (May to October), with cattle showing much higher relative abundance (RAI = 95.89) than horses (RAI = 4.37). Both cattle and horses exhibited diurnal activity patterns, with peak activity during daytime hours (Figures 4 and 5). During the cold season (November to April), livestock detections were rare, suggesting reduced activity or seasonal enclosure.

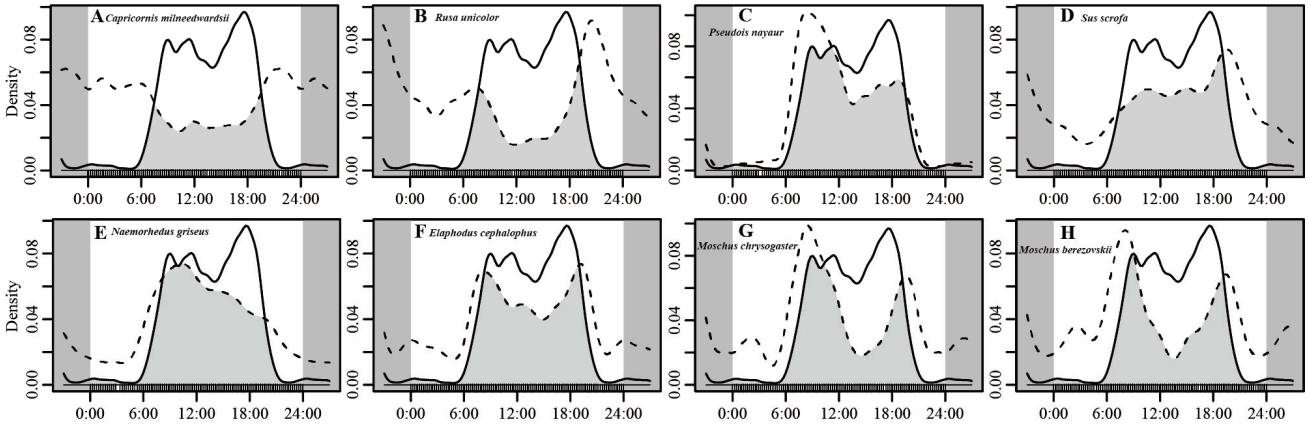

Figure 4. Daily activity rhythm overlap between cattle (solid line) and wild ungulates (dashed line. (**A**) Chinese serow, (**B**) sambar deer, (**C**) blue sheep, (**D**) wild boar, (**E**) Chinese goral, (**F**) tufted deer, (**G**) alpine musk deer, (**H**) forest musk deer).

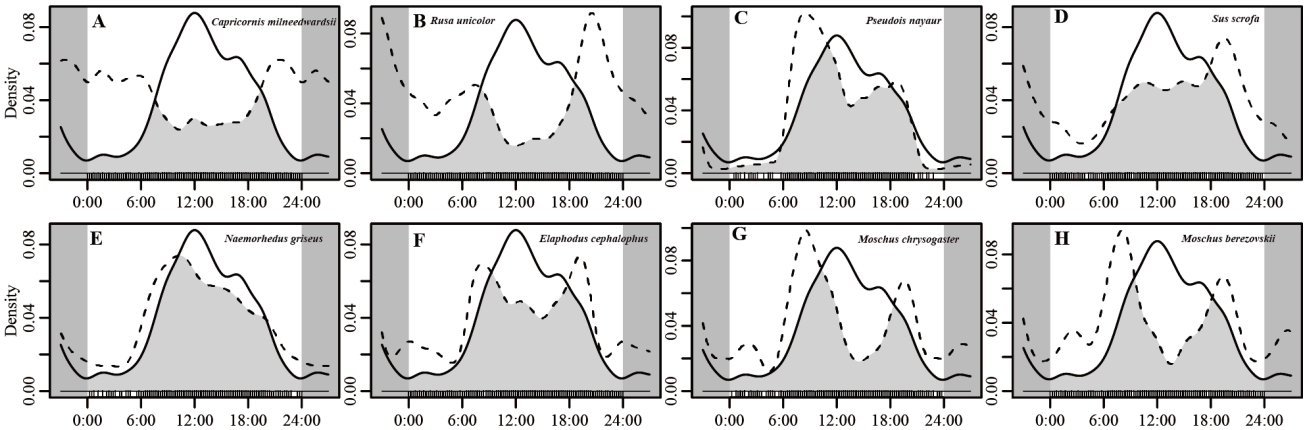

Figure 5. Daily activity rhythm overlap between horses (solid line) and wild ungulates (dashed line. (**A**) Chinese serow, (**B**) sambar deer, (**C**) blue sheep, (**D**) wild boar, (**E**) Chinese goral, (**F**) tufted deer, (**G**) alpine musk deer, (**H**) forest musk deer).

For cattle, the results indicated that (Figure 4): (1) Chinese serow (Δ_4 = 0.44, 95% CI: 0.41–0.47) and sambar deer (Δ_4 = 0.44, 95% CI: 0.41–0.48) exhibited low overlap in diurnal activity patterns with cattle; (2) forest musk deer (Δ_4 = 0.60, 95% CI: 0.56–0.64), alpine musk

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deer (Δ_4 = 0.65, 95% CI: 0.61–0.69), and wild boar (Δ_4 = 0.69, 95% CI: 0.66–0.73) showed moderate overlap with cattle; (3) Chinese goral (Δ_4 = 0.80, 95% CI: 0.75–0.85), blue sheep (Δ_4 = 0.81, 95% CI: 0.77–0.85), and tufted deer (Δ_4 = 0.73, 95% CI: 0.71–0.75) have a high degree of overlap with cattle.

For horses, the results indicated that (Figure 5): (1) Chinese serow (Δ_4 = 0.54, 95% CI: 0.48–0.61), sambar deer (Δ_4 = 0.53, 95% CI: 0.46–0.59), and forest musk deer (Δ_4 = 0.65, 95% CI: 0.58–0.72) exhibited moderate overlap in diurnal activity patterns with horses; (2) Chinese goral (Δ_4 = 0.88, 95% CI: 0.80–0.94), blue sheep (Δ_4 = 0.82, 95% CI: 0.76–0.88), tufted deer (Δ_4 = 0.79, 95% CI: 0.72–0.84), alpine musk deer (Δ_4 = 0.70, 95% CI: 0.63–0.77), and wild boar (Δ_4 = 0.77, 95% CI: 0.70–0.83) showed a high degree of overlap with horses.

4. Discussion

The impact of human disturbance on wildlife has garnered significant attention from conservationists. Grazing, one of the most prevalent forms of human disturbance, occurs in most regions globally [9]. As an essential component of terrestrial ecosystems, the ecological status of wild ungulates has also been a focus of scholarly interest. Free-ranging livestock may, to some extent, act as competitors to wild ungulates [56,57] and can influence the spatiotemporal activity patterns of wild ungulate species [23,58]. Our study found that the spatiotemporal activities of wild ungulates in Xinlong County may be affected by some extent by grazing activities, highlighting the need for further attention to this issue.

The impact of grazing activities on wildlife habitats has been extensively documented, providing a foundation for understanding the behavioral responses of ungulates. Research indicates that livestock such as cattle and horses significantly affect vegetation communities through grazing and trampling, and overgrazing leads to the degradation of herbaceous plants [6]. This causes ungulates to avoid affected areas [23,59], resulting in decreased densities of wild ungulates [60]. A study in the Northeast Tiger and Leopard National Park found that increased cattle activity reduced habitat use by wild boar and roe deer and led to avoidance by sika deer (*Cervus nippon*) [58]. Our study on ungulates in Xinlong revealed that the potential suitable habitat distribution for blue sheep was primarily influenced by livestock activity (Table S3), with suitability decreasing as livestock activity increased (Figure 3). Similar findings have been reported for blue sheep in the Gongga Mountains and the Himalayas [30,61]. Spatial interaction analysis indicated that blue sheep maintain spatial independence from cattle (SIF = 1.00), corroborating the impact of livestock on the suitability of blue sheep habitats.

The coordination and complementarity of spatiotemporal niches can promote regional species coexistence [28,62], and the relationship between wildlife and livestock is no exception [63]. Our results found that blue sheep maintain spatial independence from cattle while exhibiting high temporal overlap. In contrast, ungulates whose habitat suitability is highly positively correlated with livestock tend to show moderate or low activity overlap with livestock (Figures 3–5). These patterns suggest that ungulates may adjust their behavior in response to environmental conditions, and that high-intensity grazing could exert pressure on their habitat use and activity patterns. In contrast, in the Giant Panda National Park, where grazing also occurs, ungulates like the Chinese goral and forest musk deer coexist spatially with livestock [64]. Thus, these ungulates have adjusted their diel activity patterns to avoid livestock while ensuring their survival (Figures 4 and 5) [29]. Our data showed that most sites have livestock activity, indicating that few areas are entirely unaffected by grazing. Therefore, ungulates must adapt their spatiotemporal activities, such as maintaining spatial independence and avoiding peak livestock activity times. However, our results revealed some exceptions. For instance, blue sheep not only co-occurred spatially with horses but also exhibited a high degree of temporal overlap

(Figure 5). We speculated that this may be due to the relatively low number of horses (RAI = 4.37; compared to cattle RAI = 95.89), which likely had a minimal impact on the wildlife.

In addition to the impact of livestock activities on wild ungulates, we also found that human disturbances such as settlements and temples affect habitat suitability (Figure S1). For example, the habitat suitability of Chinese serow decreased with increasing distance to settlement (DTS, 17.13%), and for sambar deer, it decreases with increasing distance to temple (DTT, 20.09%). For forest musk deer, habitat suitability is lowest within a 10–20 km range from temples (10.09%). Influenced by traditional culture, local villagers exhibited high tolerance towards wildlife [32]. Therefore, we observed that some ungulates preferred to inhabit areas around settlements and temples. Numerous studies emphasized the protective role of sacred mountains and forests in the Tibetan regions of China for wildlife [32,65]. A recent study on birds of the whole Qinghai–Tibet Plateau has shown a significant positive correlation between Tibetan Buddhist monasteries and avian biodiversity [66]. Due to Buddhist and indigenous religious beliefs, Tibetan villagers largely adhere to a "no killing" philosophy. Additionally, considering Xinlong hosts various large carnivores, human activity areas inadvertently provide some protection for these ungulates, known as the "human shield" hypothesis [67]. Previous research has shown that carnivores tend to avoid human presence [32]. According to unpublished interview data collected during fieldwork, wild boars, sambar deer, and Chinese serow are the primary ungulates reported to cause damage to farmlands in Xinlong, consistent with their tendency to occur near villages, particularly during the warm season. Wildlife damage to local communities may affect villagers' enthusiasm for wildlife conservation and should be closely monitored.

In this study, we leveraged existing research [19,20,23,24] and applied relevant models and methods to analyze the impact of livestock on the spatiotemporal activity patterns of ungulates. Both ensemble species distribution models (ESDMs) and occupancy models have shown significant strengths and potential in ecological research [37,50]. However, it is important to recognize certain limitations that merit consideration. For example, in the two-species occupancy model, the results provide only indirect evidence of interspecific competition and cannot definitively rule out the influence of other factors [49], such as predation or intra-guild competition among ungulates. Additionally, when considering impacts at the community or ecosystem level, the effects of livestock on ungulates may vary. These challenges are inherent to the current state of research in this field. We suggest that future studies should build on the existing findings and employ novel methods, such as joint species distribution models [68] and structural equation modeling [51], to investigate the effects of human disturbances, interspecific competition, predation, and other factors on species within ecological communities.

Xinlong is a traditional pastoral area in China, with a long history of livestock presence that likely has profound impacts on wildlife. Our study analyzed the spatiotemporal interactions between livestock and wild ungulates and found significant effects of livestock on ungulates, particularly blue sheep. The impact of livestock on wildlife extends beyond spatiotemporal activity to deeper effects on the entire community. Additionally, the spread of parasitic diseases by livestock can severely affect ungulate populations [69,70]. Given the long history of grazing, it is possible that wildlife has adapted to the presence of livestock. However, Xinlong County's situation is not unique; it reflects broader patterns observed across the Qinghai–Tibet Plateau. The Plateau and its surrounding regions are home to diverse ungulate species [31,71] and have a long history of grazing [72,73]. Most of these areas experience ongoing livestock activities, with some regions even facing overgrazing. The scientific community has shown significant interest in the impacts of grazing on the Qinghai–Tibet Plateau. Thus, further investigation is needed to determine the appropriate livestock numbers in Xinlong and, by extension, across the Qinghai–Tibet Plateau. It is

crucial to balance the preservation of wildlife with maintaining a sustainable livestock population [73,74] to ensure harmonious coexistence between humans and nature.

5. Conclusions

Grazing may negatively affect wild ungulates in Xinlong County, with effects varying among species and between cattle and horses. Spatially, most ungulates tended to avoid livestock, whereas blue sheep and Chinese serow co-occurred with horses, and forest musk deer showed spatial avoidance of horses. Temporally, several ungulates exhibited low to moderate overlap in daily activity patterns with cattle, suggesting temporal partitioning as a potential strategy to reduce direct encounters. Blue sheep appeared particularly sensitive to grazing pressure, with their habitat suitability decreasing in areas of higher livestock activity. These findings highlight that livestock may influence the spatiotemporal activity of wild ungulates, underscoring the need to consider grazing management in conservation planning.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d18040227/s1, Table S1: Results of the correlation test for environmental variables based on Spearman correlation analysis. Table S2: The candidate models of two-species occupancy model. Table S3: Contribution percentages of environmental variables based on the ensemble modeling for predicting different wildlife outcomes in Xinlong; Table S4: The results of single-species occupancy models selection results for ungulate and livestocks in warm season in Xinglong; Table S5: The results of two-species occupancy models for ungulates and livestock in warm season in Xinglong; Figure S1. Response of potential suitable habitat distribution of different ungulates to disturbance factors by using ensemble species distribution models.

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Abbreviations

The following abbreviations are used in this manuscript:

ELE	Elevation
ASP	aspect
SLP	slope
TRI	terrain roughness index
DTW	Distance to water source
EVI	Enhanced vegetation index
DTD	Distance to road
DTS	Distance to settlement

DTT	Distance to temple
Ls	Livestock activity probability
ESDMs	Ensemble species distribution models
GLM	Generalized linear model
GAM	Generalized additive model
GBM	Generalized boosted regression model
CTA	Classification tree analysis
RF	Random forest
MaxEnt	Maximum entropy model
AUC	Area under the curve
MSS	Maximized the sum of sensitivity and specificity

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Behavioural Patterns and Responses of White-Faced Capuchins (*Cebus imitator*) Under Contrasting Ecotourism Pressures in Tortuguero National Park: Preliminary Findings and Management Implications

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Abstract

Ecotourism in protected areas creates a conservation paradox: tourism revenue funds protection, yet tourism infrastructure simultaneously degrades the wildlife it protects. We examined this paradox in white-faced capuchins (*Cebus imitator*) in Tortuguero National Park, comparing behaviour across a high-tourism accommodation site (2152 monthly guests) and a strictly regulated terrestrial trail. Using focal animal and sweep sampling methods, we recorded 477 behavioural units across 261 min, analysing locomotion, feeding, and agonistic behaviours through generalized linear models. Primates in accommodation areas exhibited significantly reduced high substrate use ($p = 0.005$), showed a trend toward increased anthropogenic food reliance ($p = 0.070$), and higher—but not statistically significant—rates of agonistic behaviours ($p > 0.05$). The negative correlation between natural foraging and active food supply ($r = -0.31$) is consistent with anthropogenic provisioning that may alter primate ecological functions. These findings demonstrate that effective conservation in tourism contexts requires integrated management addressing three interconnected challenges: (1) habituation to human presence, (2) food provisioning with cascading consequences, and (3) ecosystem-level degradation through altered primate functions. We recommend evidence-based interventions including secured waste management, enforcement of wildlife feeding prohibitions, and environmental education programs with community participation. Ecotourism sustainability requires managing human–wildlife interactions and integrating local stakeholder perspectives to preserve animal welfare and ecosystem functions essential for conservation.

Keywords: protected area management; ecological sustainability; wildlife tourism impacts; tourism management strategies; primate behavioural ecology; human–wildlife conflict; anthropogenic pressure; ecosystem functions; wildlife habituation

1. Introduction

Nature tourism is not always an effective conservation strategy. Although designed to support conservation, ecotourism can, in practice, harm ecosystems. Studies demonstrate that visitation inevitably produces environmental impacts, with wildlife being the primary

recipients of these effects [1]. Specifically, poorly managed human–wildlife interactions can lead to harmful practices such as food provisioning, which causes disease transmission, behavioural and ecological changes, and mortality in individuals. Food availability influences how much time animals spend on daily activities and affects how long they remain in forest habitats. Moreover, excessive habituation to human presence can increase wildlife vulnerability to harm, though the severity of these responses varies considerably across species and may be mitigated through species-specific management strategies [2]. While ecotourism is often undermined by inadequate regulation, the underlying concept retains genuine conservation potential when effective management and regulatory oversight are established [3]. According to optimal foraging theory, animals must balance energy intake with the need to avoid predators and reproduce. When humans provide food, animals reduce their movement in search of natural resources, leading to behavioural alterations. In primates, these changes may include increased aggression to obtain food and behaviours such as stealing personal belongings from visitors to use as bargaining tools for food rewards. Research on token-based exchanges demonstrates that monkeys and great apes use objects symbolically to request specific food rewards [4,5]

For the *Cebus* genus specifically, food provisioning is the primary driver of human–primate conflict [6]. Human presence represents a critical factor for primate populations and must be carefully evaluated due to its potential influence on health, behaviour, and long-term species viability [7]. Furthermore, humans introduce pathogens into forest habitats that can be transmitted to primates. Primates in high-tourism areas may exhibit poorer health than those in undisturbed areas, as documented in howler monkeys [8] and observed in white-faced capuchins [7]. Altered nutritional intake from anthropogenic food can negatively impact primate health and may have long-term consequences for survival and reproduction. Additionally, provisioning reduces the time troops spend foraging, thereby altering faunal communities and ecosystem processes. For example, reduced foraging can decrease seed dispersal, a key ecological function uniquely provided by primates in tropical forests [9]. Provisioning by humans fundamentally alters primate ecological functions, including seed dispersal and plant–primate interactions critical for tropical forest regeneration [10], underscoring the importance of examining these impacts in tourism contexts.

Building on this conceptual background and the conservation challenges identified in the region, we focus on how contrasting tourism settings within Tortuguero National Park are associated with changes in the locomotion, feeding, and agonistic behaviour of *Cebus imitator* between a high-tourism accommodation complex and the more strictly regulated Jaguar Trail. In order to structure this analysis, we formulated the following hypotheses:

H1. *We hypothesize that primate behaviour and ecology differ significantly between accommodation areas and the Jaguar Trail due to differences in human presence, conservation regulations, and resource availability. We predict stronger behavioural impacts in the accommodation area (characterized by higher anthropogenic food availability, weaker conservation enforcement, and closer proximity to human structures) compared to the Jaguar Trail (under stricter regulations and greater natural resource availability).*

H1.1. *Primate locomotion will differ between locations. Individuals will primarily use high substrates (arboreal/canopy) along the Jaguar Trail, while predominantly using lower substrates in the accommodation area where they forage for anthropogenic food sources.*

H1.2. *Diet composition will differ between locations. Primates will show greater dependence on anthropogenic food sources in the accommodation area, while natural foraging will predominate along the Jaguar Trail.*

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H1.3. *Habituation to humans will affect behavioural patterns. Primates in the accommodation area will exhibit increased agonistic behaviour and directed food interactions reflecting greater habituation to humans, compared to those along the Jaguar Trail.*

These hypotheses guided both the design of our observational protocol and the structure of the statistical analyses presented in Section 2.

This research aims to explore these dynamics through a case study on white-faced capuchin monkeys (*Cebus imitator*) in Tortuguero National Park, Costa Rica. By analysing the behavioural responses of this species to different tourism contexts, we seek to better understand the real conservation challenges posed by ecotourism in highly biodiverse environments.

1.1. Tortuguero National Park

Boca de Tortuga was the former name of the Tortuguero community when it was settled in the early 20th century. This Afro-Caribbean community was engaged in the intensive exploitation of sea turtles—for the consumption of their eggs and meat—and in logging for export. However, research by zoologist Archie Carr in the 1950s on green turtle (*Chelonia mydas*) behaviour revealed the ecological importance of Tortuguero as a major nesting site for turtles in the Caribbean. This discovery led to the conservation of the area, which was declared a National Park in 1970. The boundaries of this area have been expanded several times, with the current extent being 76,937 hectares, encompassing both marine and terrestrial areas.

Tortuguero National Park (Parque Nacional Tortuguero, henceforth TNP) is located in the northeast of Costa Rica, on the Caribbean coast. It is part of the Limón region, bordering the communities of Tortuguero and San Francisco to the north, the *Parismina* community to the south, the Caribbean Sea to the east, and the Tortuguero Lagoon to the west. Figure 1 shows the boundaries of the National Park, including both its marine and terrestrial zones.

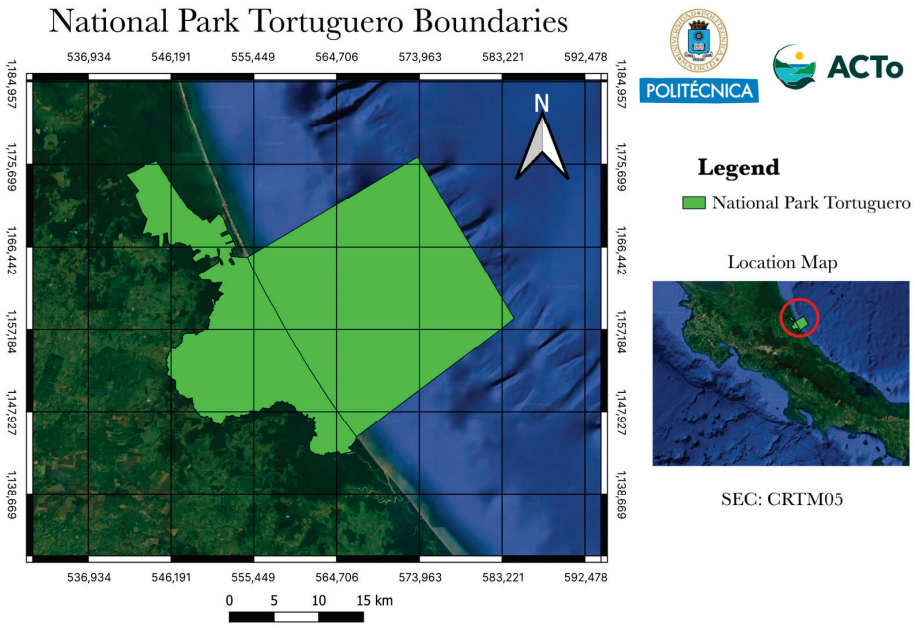

Figure 1. Location and administrative boundaries of Tortuguero National Park (TNP), a 76,937-hectare protected area on Costa Rica's Caribbean coast (Limón Province). The park encompasses marine and terrestrial zones and protects critical habitats for endangered species including manatees (*Trichechus manatus*), jaguars (*Panthera onca*), and white-faced capuchins (*Cebus imitator*), the focal species of this study.

TNP is now a key tourist destination, known for its biodiversity and its role in the conservation of marine and terrestrial species. It protects 30 km of beach crucial for the nesting of four species of sea turtles, as well as important habitats for endangered species like the manatee (*Trichechus manatus*) and the jaguar (*Panthera onca*) and for protected species like the white-faced capuchin (*Cebus imitator*). Its tropical wet and humid ecosystem, with an annual rainfall of 6000 mm and average temperatures between 25 °C and 30 °C, harbours a rich biodiversity that includes 734 plant species, 442 bird species, 138 mammal species, 118 reptile species, 58 amphibian species, and 460 arthropod species [11]. The community of Barra de Tortuguero relies heavily on nature tourism. The TNP and the community are interrelated, with tourism being a crucial source of income for local residents. In Costa Rican protected areas, primates often serve as flagship species, playing a central role in attracting visitors and generating economic benefits [12]. Conservation is essential for local economic development. Environmental education programs, as well as efforts by conservation organizations, reinforce the park's role in protecting natural resources while promoting sustainable livelihoods [13]. The area was declared a National Park with the main goal of preserving tropical flora and fauna. Beyond its ecological value, TNP's water channels and lagoons hold both ecological and scenic value. The National Park designation allows the area to be used for recreational, educational, and scientific purposes. Park authorities promote the responsible development of tourism through tools such as the Management of Visitor Flow, which aims to assess tourism activities comprehensively. This tool establishes impact indicators, thresholds of change, and a monitoring system to reduce or mitigate negative effects [11].

Recent studies have explored human–primate interactions in the region. White-faced capuchin monkeys (*Cebus imitator*) exhibit behavioural plasticity ranging from increased aggression to habituation, underscoring the importance of implementing species-specific conservation strategies to mitigate potential conflicts [2].

1.2. Cebus imitator

Our study species, commonly known as the white-faced capuchin, white-faced monkey, or white-headed monkey (Figure 2), belongs to the taxonomic subfamily *Cebinae* and to the commonly named New World monkeys. Cebines are easily recognizable due to their long-time use in the film industry, presence in the pet trade, and use in street performances. White-faced capuchin monkeys (*Cebus imitator*), formerly known as *Cebus capucinus*, are diurnal and mostly arboreal [14]. They live in a variety of habitats throughout Central America, including the wet lowlands forests on the Caribbean Coast and deciduous dry forest on the Pacific coast of Costa Rica. Capuchins weigh from 2.5 to 3.5 kg, with females being slightly smaller than males, and they measure between 80 and 90 cm in length, including the tail. Their diet is mainly omnivorous, including insects, ripe fruits, frogs, lizards, and squirrels, with food choices changing according to season. White-faced capuchins spend 70–80% of the day foraging and travelling, forming troops of about 30 individuals [14]. Beyond their primarily frugivorous diet, capuchins are recognized for their sophisticated behavioural repertoire, including tool use and problem-solving abilities [15], which may explain their relatively high capacity for adapting to anthropogenic environments and their susceptibility to habituation.

This species is important in seed dispersal and their main predators are humans, raptors, large snakes, and felines. These primates often live up to 40 years of age in the wild, with the oldest recorded individual reaching 54 years in captivity. *Cebus imitator* faces several conservation threats, including pet trade, deforestation (habitat destruction), and hunting by farmers.



Figure 2. Male adult *Cebus imitator* (white-faced capuchin) from Tortuguero National Park. The species exhibits distinctive white facial markings, small body size (2.5–3.5 kg), long prehensile tail, and sophisticated tool use and problem-solving abilities. These behavioural and morphological traits correlate with high adaptability to anthropogenic environments and susceptibility to habituation in tourism contexts (reproduced with permission from Ms. Alice Lapeyre, 2022).

2. Material and Methods

A general assessment of the initial situation was carried out through a literature review of the state of the art, expert consultations, and interviews with locals and tourism sector workers. This research was conducted in compliance with Costa Rican Wildlife Conservation Law (No. 7317) and Tortuguero National Park (TNP) management regulations. Fieldwork consisted exclusively of non-invasive observational studies with no animal handling. Research access was formally approved by the Área de Conservación Tortuguero (Sistema Nacional de Áreas de Conservación, SINAC; Ministerio de Ambiente y Energía, MINAE) through authorization SINAC-ACTo-DASP-PNT-EPTS007-2022. A sample of nine hotels was selected to assess various conservation-related variables, including monthly visitor numbers, the degree of structural immersion within the forest, connectivity through natural or anthropogenic elements (e.g., cables), and food and beverage accessibility. The latter was evaluated based on restaurant infrastructure, food storage practices, and waste management systems. In addition, surveys were conducted in these hotels to assess human–primate interactions, aiming to determine in which establishments such interactions occurred, which primate species were involved, and the behavioural patterns exhibited by the animals during these encounters.

Based on this preliminary work, two key sites were selected for behavioural monitoring. The objective was to compare the behaviour of individuals of the primate species *Cebus imitator* in two different tourism-use scenarios. A field study was conducted between June and November 2022 to observe and compare primate behaviour in these two areas within TNP.

2.1. Study Area

To contextualize the study's methodology and development, it is essential to understand the tourism offerings and infrastructure established in *Tortuguero.* Tourism in the community is a significant determinant of biodiversity conservation. TNP is the main tourist attraction in the community, attracting both national and international visitors. Key activities include motorboat, kayak, or canoe tours through the park's canals, a nighttime

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turtle nesting tour, rainforest hikes and wildlife observation. These activities take place in settings such as the terrestrial Jaguar Trail, various water channels (*Caño Harold*, *Caño Mora*, *Caño Chiquero*, *Caño Palma* and *Río Tortuguero*), and *Cuatro Esquinas* Beach. In addition to TNP, there are complementary tourism offerings outside the park, such as nighttime nature tours, sport fishing, dining at the floating *Katonga* restaurant, and canopy tours at local hotels.

Accommodation services in *Tortuguero* are divided into two main categories. The first includes hotels and cabins primarily aimed at independent travellers, typically offering more affordable prices, and located in the town. The second category includes lodges, which attract a higher volume of guests and have direct commercial ties with wholesalers, tour operators, and airlines.

They also offer a greater number of services and are located along the canals, generally further away from the population centre. Lodges differ from regular hotels in that they are accommodations located in hard-to-reach areas, deep within the jungle, mountains, or strategic locations such as lagoons and rivers. The study will focus on this type of establishment due to their dimensional characteristics and significant integration into natural environments, which pose a greater risk of habituation for wildlife [2,10]. The cartographic figures included in this study were prepared using QGIS (v3.28).

An accurate description of the two study scenarios, where the comparison of monkey behaviour took place, is essential:

2.1.1. The Jaguar Trail

This is the only operational terrestrial walking trail currently available in TNP (hereafter the Jaguar Trail). It runs parallel to the beach and is used both by the public and by park rangers for monitoring and protection purposes (Figure 3). The trail covers a total distance of 2 km one way, making a total of 4 km for the round trip. It is marked every 100 m with numbers starting from 37 and ending at 60, which delineates the boundary of the park's public use area. Each of these markers provides access to the beach. Additionally, as the trail is situated within the jungle, it offers opportunities to observe various wildlife species, including monkeys, agoutis, sloths, snakes, and iguanas, among others. This trail experiences less human interference due to the stricter regulations within TNP, which include prohibitions on construction and the introduction of food and beverages into the park. In addition to the prohibition on bringing food onto the trail, some studies [2] indicate that tourists may break this rule due to their increased interest to interact with wildlife in natural areas.

Its track is depicted in Figure 3, which was generated from coordinates recorded every 100 m using a Garmin eTrex 22x global positioning system (GPS) device (Garmin Ltd., Olathe, KS, USA).

2.1.2. Evergreen Lodge and Rana Roja Lodge

These two tourist accommodations, Evergreen Lodge and Rana Roja Lodge, constitute a single territorial unit, despite being separate establishments. They share the same spatial boundary and are located on a small land islet across from the main land bar where the Tortuguero community is situated. This islet connects directly to the terrestrial boundaries of TNP, forming a biological corridor. Together, they host approximately 2152 guests per month during the high season, which coincides with the study period. As part of an initial assessment to identify scenarios with the greatest anthropogenic pressure on primates, we conducted visits and surveys in nine hotels (Figure 4). We evaluated various parameters, including the number of tourists per month, the presence of sustainable management certifications, degree of immersion in the forest, ecological connectivity, ac-

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cessibility of food and drink to wildlife, organic waste management, and the availability of environmental information. This analysis revealed that Evergreen Lodge and Rana Roja Lodge concentrate high levels of human–wildlife interaction pressure. Together, the two hotels rank second among all those studied in attracting tourists, with a total of 2152 during the high season (July and August). It was also observed that food and beverage accessibility in the hotels was high. They were the only establishments that, during interviews with local residents and tourism workers, were repeatedly mentioned as frequent observation sites for white-faced capuchins (*Cebus imitator*) and as locations where regular interactions between monkeys and guests were perceived as a recurring management issue. Moreover, *Cebus imitator* is a species that tends to approach humans and their facilities, indicating a high capacity for habituation [2]. Finally, and to prevent the normalization of feeding wildlife even outside protected areas, we consulted the relevant legislation [16]. Article 116 explicitly establishes the prohibition of feeding wildlife throughout the entire national territory.

Finally, Figure 5 provides a clear representation of the spatial relationship between the two sampling sites, indicating the position of the Jaguar Trail relative to the hotel complex.

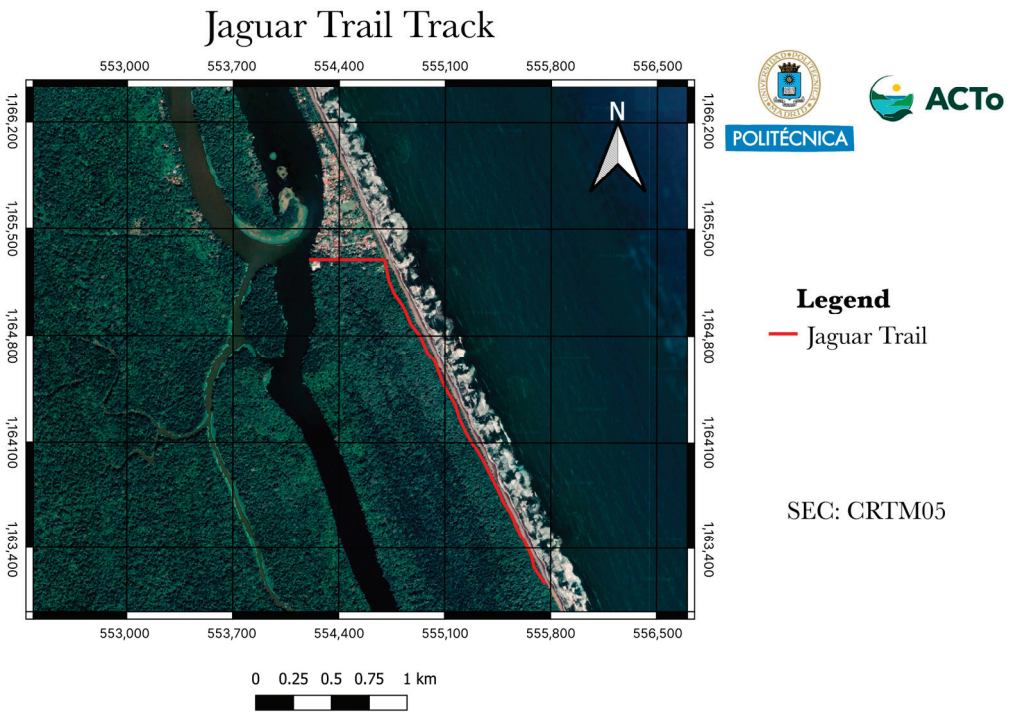

Figure 3. Geographic representation of the Jaguar Trail (red line), the only operational terrestrial trail in Tortuguero National Park. The 4 km round-trip trail (2 km one-way) runs parallel to the Caribbean beach, demarcated by numbered markers every 100 m (markers 37–60), with beach access points at each marker. The trail is situated within primary tropical rainforest and provides wildlife observation opportunities. GPS coordinates were recorded at 100 m intervals using a portable GPS device during survey work. The Jaguar Trail experiences less human interference due to strict TNP conservation regulations prohibiting construction and food/beverage introduction.

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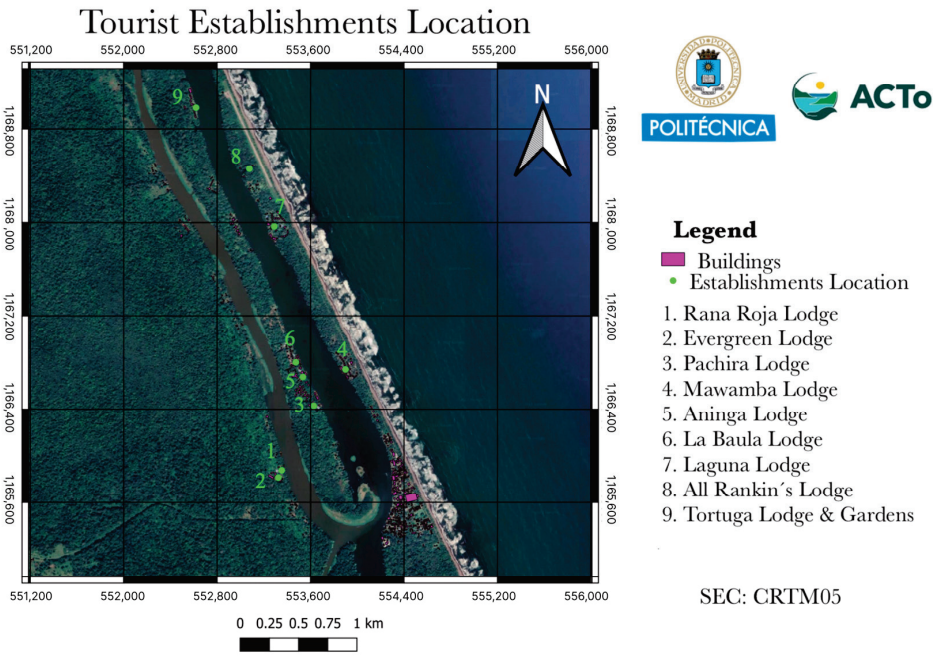

Figure 4. Spatial map of Tortuguero showing location of accommodation establishments evaluated for human–primate interaction pressure (n = 9 hotels surveyed). Study sites are indicated as (1) Rana Roja Lodge and (2) Evergreen Lodge, two adjacent lodges located on a small land islet forming a biological corridor directly adjacent to TNP boundaries. These establishments were selected based on highest tourism volume (2152 guests/month), greatest food accessibility to wildlife, maximum forest immersion, and documented capuchin interactions. The map illustrates the strategic location creating intense human–wildlife interface compared to the strictly regulated Jaguar Trail.

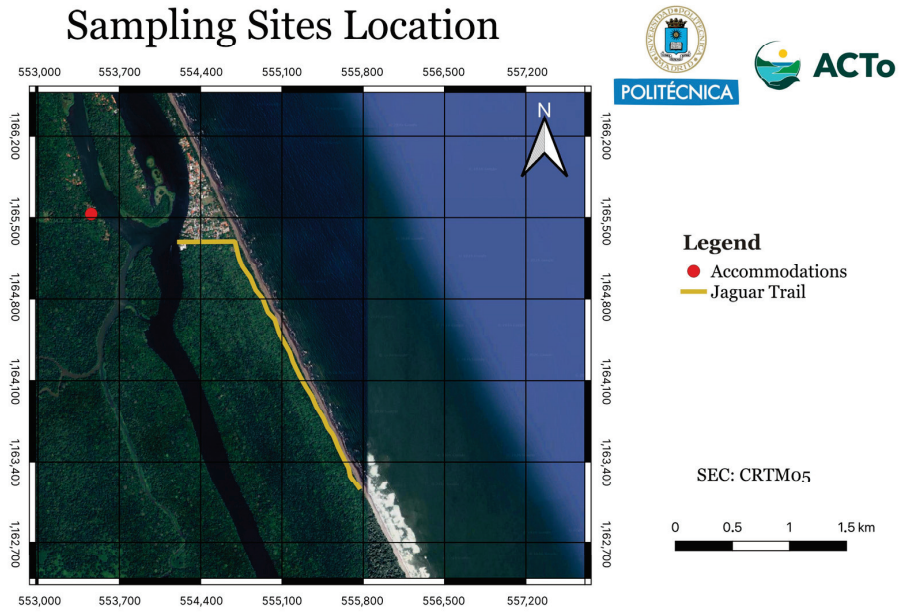

Figure 5. Spatial relationship between the two sampling sites in Tortuguero. The red point marks the Evergreen–Rana Roja hotel complex on a small land islet adjacent to Tortuguero National Park, while the yellow line represents the 4 km Jaguar Trail running parallel to the Caribbean coast. The lagoon and river channels clearly separate the accommodation area from the terrestrial walking trail, making it unlikely that the same *Cebus imitator* troops regularly use both sites within a single day. This map is intended to illustrate the strong environmental contrast between the accommodation–forest interface and the protected forest trail sector of the park.

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2.2. Sampling Design

Data were collected by Janire Sánchez, a trained observer who completed the field practicum as part of her master's degree in Sustainable Ecological Tourism Management. To compare behavioural patterns of *Cebus imitator* between the accommodation area and the Jaguar Trail, we used a standardized ethogram (Table 1). Ethogram-based approaches are well-established methodologies for quantifying behavioural frequencies in primatological studies, particularly for comparing behavioural variation across different environmental contexts [6,7]. The ethogram was designed to incorporate behavioural categories organized into five functional classes—socialization, locomotion, rest, feeding, and agonistic behaviours—selected to characterize behavioural responses of *Cebus imitator* to tourism pressure and human provisioning [7]. These categories enabled us to distinguish between natural foraging activities and anthropogenic food consumption (active and passive supply), as well as assess habituation levels reflected in agonistic behavioural responses. Observations were conducted using Nikon Monarch M5 8x42 binoculars (Nikon Corporation, Tokyo, Japan) to view canopy-dwelling individuals, and a Casio HS-80TW stopwatch (Casio Computer Co., Ltd., Tokyo, Japan) was used to record the precise timing of observation intervals. We employed sweep sampling to record behavioural unit frequencies at the group level, capturing overall group activity and spatial organization across study sites [7]. When we identified a troop, continuous observations lasted 20 min. If the troop moved away, observation stopped, and departure time was recorded.

Table 1. Comprehensive ethogram of behavioural categories and units recorded during primate behavioural observations (n = 14 observation days, 261 min total). The ethogram comprises 16 behavioural units organized into five functional categories: socialization (grooming together, auto-grooming, play), locomotion (jumping, high walk, low walk), rest (sleep, stand, motionless), feeding (foraging, active supply, passive supply), and agonistic behaviours (threaten, joint threaten, assault). Categories were adapted from established primatological methodologies and specifically designed to assess behavioural responses of *Cebus imitator* to differential tourism pressure and human food provisioning between accommodation sites and the strictly regulated Jaguar Trail [6,7].

Type of Behaviour	Behavioural Unit	Description of the Activity
Socialization	GROOMING TOGETHER (GT)	An individual lies on its side on a substrate with its back towards another individual(s) who grooms the first one by removing debris and ectoparasites with their hands, tongue or teeth.
	AUTO-GROOMING (AG)	Individual sits on a substrate and uses its upper limbs to remove debris and ectoparasites from its body.
	PLAY (P)	One monkey chases another until it manages to grab it, and they begin a brief physical interaction (approx. 5 s) before resuming the chase.
Locomotion	MOVE BY JUMPING (J)	Individuals move across substrates by jumping.
	HIGH WALK (HW)	Individuals walk on two or four legs on the substrates above the ground.
	LOW WALK (LW)	Individuals walk on two or four legs on the ground.

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Table 1. *Cont.*

Type of Behaviour	Behavioural Unit	Description of the Activity
Rest	SLEEP (SL)	Individuals lie on the substrate and remain still with their eyes closed, with minimal movement.
	STAND (ST)	Individuals lie on the substrate, keeping two or three of their limbs relaxed and open, remaining still with minimal movement.
	MOTIONLESS (MOT)	Individuals remain in the same spot on the substrate, generally sitting, moving their body slightly without leaving the point where they are located.
Feeding	FORAGING (FO)	Individuals manipulate leaves, sticks, and other natural substrates in search of their natural food, or consume items located during this search.
	ACTIVE SUPPLY (AS)	Individuals searching for and eating processed food or fruit from tables and bags (opened by hand) belonging to tourists.
	PASSIVE SUPPLY (PS)	Individuals feed on processed food or fruit given to them by tourists. These are offered directly to them, and the monkeys reach out their hands to take the food when the tourist puts it in their mouth or places it nearby.
Agonistic	THREATEN (T)	Individuals on all fours vocalize, show their teeth, raise their hair and raise their tails. They may rock their bodies from side to side or shake branches.
	JOINT THREATEN (JT)	One monkey rides on another's back, placing their heads one on top of the other, and both vocalize, show their teeth, raise their hair, and raise their tails.
	ASSAULT (A)	An individual uses one or both of its front legs to hit, kick, or push another individual.

We sampled systematically between the two scenarios during July, August, September, and October 2022, conducting observations during morning (7:00 AM–11:00 AM) and afternoon (12:00 PM–5:00 PM) sessions to capture the primary activity periods of *Cebus imitator*. Specifically, the dataset included observations conducted on the following days and during the corresponding hours (Table 2).

Additionally, we visited the accommodation with morning visits on 15 and 24 September, but we did not find any troops. We also visited the Jaguar Trail on 16, 19, 26 September and 1 and 5 October, but we did not find any individuals.

The studied species, *Cebus imitator*, is diurnal and forms part of a complex social structure referred to as a troop. Observed troops were usually composed of 12 to 15 individuals, commonly including one or two adult males.

2.3. Statistical Analysis

Statistical analyses and data visualisations were conducted in Python (v3.12.9) using pandas (v2.3.0), NumPy (v1.26.4), SciPy (v1.16.2), statsmodels (v0.14.6), matplotlib (v3.10.3), and seaborn (v0.13.2).

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Table 2. Detailed survey dataset for primate behavioural observations conducted in Tortuguero National Park during June–October 2022. Data include observation date, location (accommodation sites: Evergreen Lodge and Rana Roja Lodge; Jaguar Trail), time of visit (morning 07:00–11:00 AM or afternoon 12:00–17:00 PM), duration of continuous observation (minutes:seconds), and troop composition (number of individuals observed per sampling session). Total dataset comprises 25 survey days (14 successful observations yielding 261 min of behavioural recordings and 477 behavioural units; 11 no-encounter days). Sampling was systematically distributed across both sites to balance effort and capture seasonal variation in visitor pressure.

Date	Location	Time of Visit	Duration	Sample Size
27 July	Accommodation	Morning visit	9:10–9:20 h	11 individuals troop
3 August	Accommodation	Morning visit	7:40–7:45 h	7 individuals troop
26 August	Jaguar Trail	Afternoon visit	14:35–14:37 h 16:05–16:08 h	6 individuals in the first period. 10 individuals in the second period
12 September	Jaguar Trail	Morning visit	8:38–8:58 h	2 individuals
13 September	Jaguar Trail	Morning visit	9:00–9:20 h	6 individuals troop
17 September	Jaguar Trail	Morning visit	9:13–9:17 h 9:24–9:31 h 10:19–10:39 h	3 individuals in the first two periods. 2 individuals in the third period
20 September	Accommodation	Afternoon visit	12:17–12:57 h 13:30–13:50 h	9 individuals troop
21 September	Jaguar Trail	Morning visit	9:00–9:20 h	11 individuals troop
22 September	Accommodation	Afternoon visit	13:45–13:55 h	4 individuals troop
23 September	Jaguar Trail	Morning visit	9:42–9:47 h 10:10–10:14 h 10:16–10:22 h	One individual in each period
27 September	Accommodation	Afternoon visit	13:09–13:15 h 13:27–13:47 h	One female in the first period. One individual in the second period
29 September	Accommodation	Afternoon visit	13:17–13:37 h	3 females and one male.
30 September	Jaguar Trail	Morning visit	8:26–8:35 h	4 individuals troop
6 October	Accommodation	Afternoon visit	13:32–13:52 h	5 individuals troop

As mentioned previously, individual animals could not be reliably identified across sampling days. This means that some individuals may have been observed more than once, introducing the possibility of non-independence (autocorrelation) in the dataset. Because individual identity could not be included as a random effect, mixed-effect models were not feasible. Instead, we analysed behavioural counts using Generalized Linear Models (GLMs), which are appropriate for modelling count data, such as Poisson or Negative Binomial distributions. A GLM relates the expected value of the response variable—here, the counts of specific behaviours—to explanatory variables using a suitable probability distribution. Behavioural counts YijPoisson(ij) were modelled using a Poisson GLM with a log link, such that,

$$\log\left(\mathrm{E}\left[\mathrm{Y}_{ij}\right]\right) = \beta_0 + \beta_1 \mathrm{Location}_{ij} + \beta_2 \mathrm{TimeofDay}_{ij} + \beta_3 \mathrm{GroupSize}_{ij} + \log(\mathrm{Duration}_{ij})$$

Observation duration (in minutes) was included as an offset to standardize behavioural counts to per minute rates and account for differences in sampling effort. Location was included as the main fixed effect of interest, with accommodation treated as the reference category, while time of day and group size were included as covariates to control for

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potential confounding effects. Model dispersion was assessed by comparing the Pearson chi-square statistic to its degrees of freedom, with values near or below one indicating adequate fit of the Poisson model. Effect sizes are reported as incidence rate ratios (IRRs) with 95% confidence intervals, representing rate contrasts relative to the reference category. For behaviours exhibiting structural zeros in some locations, Fisher's exact tests were used for presence–absence comparisons, for which IRRs are not defined.

3. Results

The dataset comprised 25 survey days, of which primates were observed on 14 days, for a total of 4 h and 21 min (261 min) recording 477 behavioural units. The data were categorized into two distinct survey contexts:

- Jaguar Trail: A total of 130 min of observation yielded 234 recorded behaviours.
- Tourist Accommodation Sites (Evergreen Lodge and Rana Roja Lodge): A total of 131 min yielded 243 recorded behaviours.

3.1. Behavioural Patterns of Food Acquisition

To analyse behavioural associations, we produced a correlation matrix (Figure 6) that compares each pair of behavioural units (rows/columns) using Spearman rank correlation values. Spearman correlation is a nonparametric, rank-based measure that is appropriate for our discrete and skewed behavioural counts, as it does not require normally distributed data and captures monotonic associations between behaviours. High positive correlations (red) indicate that the two behaviours frequently co-occurred within the same observation period, whereas low or negative correlations (blue) suggest that the presence of one behaviour typically excluded the presence of the other.

In the correlation matrix (Figure 6), several intuitive patterns emerge. Auto-grooming (AG) tends to co-occur with grooming together (GT), motionless behaviour (MOT), and standing, and is less frequent when agonistic behaviour is present, indicating that the matrix captures biologically meaningful associations.

Concerning food acquisition patterns, the following correlations emerged:

- Foraging (FO), highlighted by the green squares, was positively correlated with high walk (HW; r = 0.73) and auto-grooming (AG; r = 0.58), and negatively correlated with threatening (T; r = −0.52).
- Active supply (AS), marked in purple, was positively correlated with low walk (LW; r = 0.52) and joint threatening (JT; r = 0.50), and showed a weaker positive correlation with individual threatening (T; r = 0.29). In addition, it was negatively correlated with foraging (FO; r = −0.31).

Interestingly, no occurrences of assault, sleeping individuals, or passive supply were recorded during the study.

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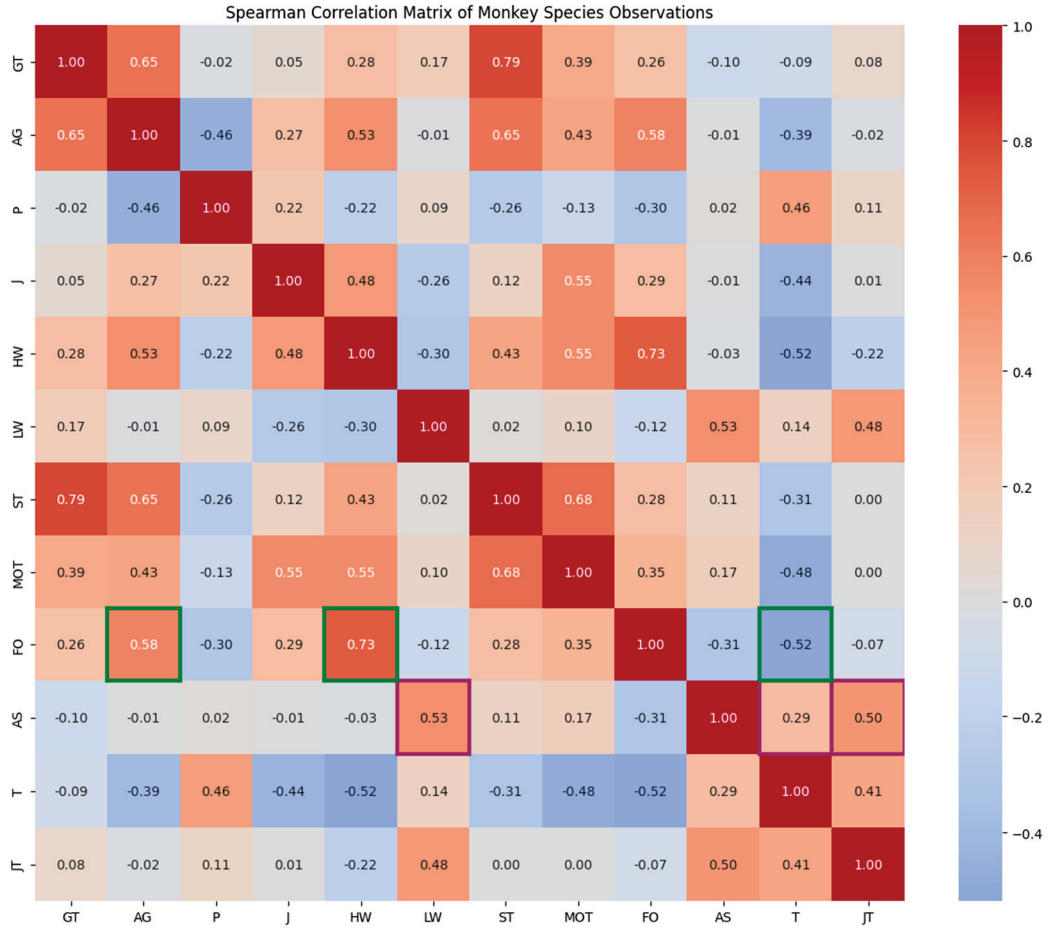

Figure 6. Spearman rank correlation matrix of behavioural variables. Red and blue cells indicate positive and negative correlations, respectively. Green-framed cells highlight correlations involving foraging (FO), including its positive association with high walking (HW; r = 0.73) and auto-grooming (AG; r = 0.58), and negative association with threatening (T; r = −0.52). Purple-framed cells highlight correlations involving active supply (AS), including its positive associations with low walking (LW; r = 0.52) and agonistic behaviours (JT r = 0.50; T r = 0.29), and its negative association with foraging (FO; r = −0.31).

3.2. Influence of Tourist Areas on Primate Behaviour

We standardized behavioural data by converting raw counts to rates and modelled them using Poisson GLMs, checking the Poisson assumption by comparing residual deviance to degrees of freedom; all dispersion ratios were at or below one, indicating no overdispersion and supporting the use of the Poisson distribution. However, some behavioural units were entirely absent in certain locations, producing structural zeros that make count-based models inappropriate. For these behaviours, we instead analysed their presence or absence using Fisher's exact tests, which better reflects the data structure when a behaviour does not occur at all in specific contexts.

Behavioural patterns across the two locations are shown in Figure 7 using violin plots, which display the distribution shape along with the minimum, mean, and maximum values. Each plot indicates the behavioural unit analysed, the statistical test used, and its corresponding value. As shown in Figure 7, Poisson GLMs were used for all behavioural units except low walk and active supply, where the absence of these behaviours on the Jaguar Trail led us to use Fisher's exact test instead. For behaviours analysed with Poisson GLMs, effect sizes (IRRs) with 95% confidence intervals are annotated directly on each

subplot. For behaviours analysed with Fisher's exact tests due to structural zeros, IRRs are not defined.

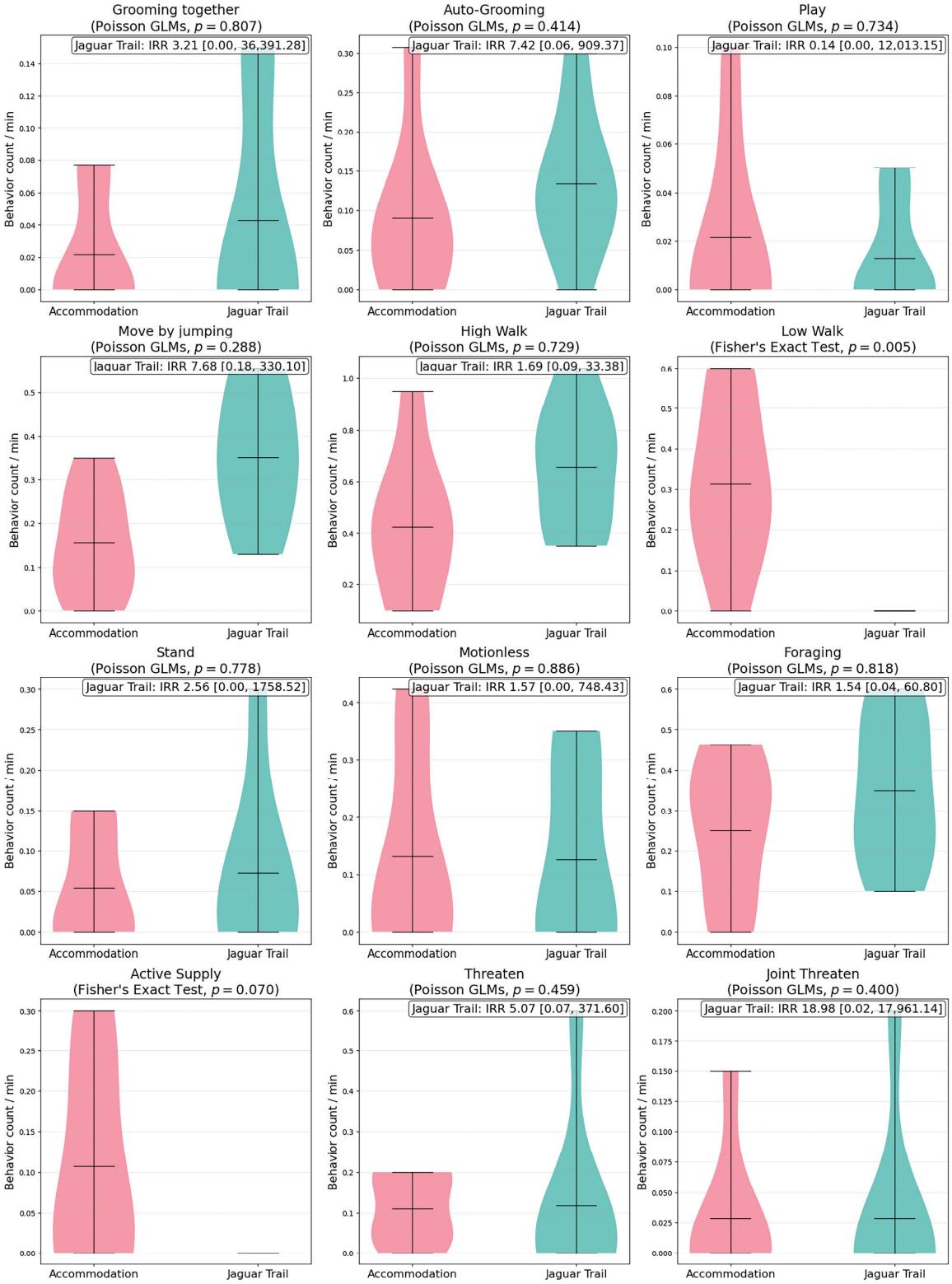

Figure 7. Comparison of behavioural units between accommodation and Jaguar Trail sites using violin plots. Plots display distribution shape with minimum, mean, and maximum values. Poisson generalized linear models were used for most behavioural variables, while low walk and active supply (absent on the Jaguar Trail) were analysed using Fisher's exact test.

Based on the analysis, the following insights were obtained:

- Regarding feeding activities, foraging was observed more frequently on the Jaguar Trail, although with the current level of sampling this difference cannot be considered statistically significant. In contrast, active food provisioning occurred exclusively at tourist accommodation sites, and the relatively low *p*-value (0.070) suggests a possible effect of location on diet composition (H1.2), although the evidence remains inconclusive.
- In terms of locomotion, high walking and jumping—both indicative of more active exploration—were more common on the Jaguar Trail, but these differences were not statistically significant (*p*-values: 0.729 and 0.288). However, low walking was found to be significantly lower on the Jaguar Trail (*p*-value: 0.005), providing partial support for H1.1 (primate locomotion differs between scenarios). This latter result suggests that, with a larger sample size, the differences observed in high walking and jumping might become detectable, although this cannot be determined from the present data.
- For agonistic interactions, both individual and joint threatening behaviours were more frequent at tourist accommodation sites than on the trail, but none of these differences reached statistical significance with the current dataset (*p*-values: 0.459 and 0.400).

4. Discussion

4.1. Interpretation of Behavioural Patterns

In this study, we hypothesized that *Cebus imitator* troops would exhibit different levels of habituation to humans depending on the scenario. Specifically, we predicted that wildlife on the more strictly regulated scenario (Jaguar Trail in TNP) would show lower habituation, whereas primates in tourist accommodations, where interactions with humans are less controlled, would exhibit higher habituation. Although behavioural data were compared between the two scenarios, it is not possible to directly attribute observed differences to human presence alone. Nevertheless, we know that the Jaguar Trail is less developed than the accommodation area, where multiple anthropogenic factors could influence primate behaviour. The following discussion interprets the results based on these contextual assumptions.

4.1.1. Locomotion

The percentage of primates observed walking on low substrates on the Jaguar Trail is zero, whereas in the accommodation, this behaviour is identified in addition to high walk.

According to literature, New World monkeys were thought to be entirely arboreal; however, wild capuchins can be quite terrestrial at times. They are bipedal and carry objects with their hands [15]. Although they are primarily arboreal, they can also walk on the ground with the objective of foraging [17] and this species is more terrestrial than other capuchin populations [15]. Although this behaviour does not always indicate an alteration in this fauna, some studies have shown that food provided by humans is a determining factor for primate troops to use the ground or low heights for their activities. Provisioning of primates by humans is known to impact their activity budgets, diets and ranging patterns. Making them more dependent on human food and less likely to forage naturally [10]. On the other hand, the positive correlations between "low walking" and "active supply", and between "high walk" and "foraging", suggest that when primates moved on low substrates they were often searching through waste or obtaining human-provided food, rather than foraging naturally. Furthermore, the comparison in Figure 7 shows significant differences in low walk behaviour between scenarios, which supports H1.1 and suggests that locomotion patterns differ across settings.

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4.1.2. Feeding

Human provisioning of wildlife with food is a widespread global practice that occurs in multiple socio-cultural contexts. Food is often provided voluntarily to animals within residential areas and temples as part of religious or cultural traditions, or at wildlife tourism sites to attract animals for viewing and photography. This practice is particularly common with primates, whose charismatic nature encourages people to feed them. However, such practices represent a potential threat to wildlife health. Consistent with previous studies, our results show that "active supply" occurred only at tourist accommodation sites, where monkeys increasingly consumed human-provided food in addition to natural resources (Figure 8A,B), indicating a shift toward anthropogenic diet supplementation and a progressive alteration of their normal foraging patterns. The effect of location on "active supply" had a relatively low p-value ($p = 0.070$), suggesting a possible location-related pattern that might become even more evident with a larger sample size. In contrast, no "active supply" was observed along the Jaguar Trail, where monkeys depended primarily on natural foraging due to the park's conservation restrictions, although they could still be fed if tourists broke the rules. Thus, we cannot claim that primates are systematically fed by humans across all contexts, but we can support the part of H1.2 indicating that "active supply" is higher in the accommodation area and the negative correlation between "active supply" and "foraging". While passive food supply (direct hand-feeding from tourists) was not directly observed during focal sampling, qualitative observations and staff interviews indicated that direct feeding occurs regularly outside formal observation periods. This suggests our quantitative assessment may underestimate total provisioning frequency.



Figure 8. Anthropogenic food-related behavioural patterns in *Cebus imitator* at accommodation sites, illustrating mechanistic links between tourism infrastructure and primate behaviour. (**A**) Individual actively obtaining a discarded plastic bag from accommodation waste, exemplifying active supply (AS) behaviour—direct acquisition of anthropogenic food sources. This demonstrates the shift from natural foraging to opportunistic consumption of human-derived resources, a key mechanism driving H1.2 (diet composition differences). (**B**) Individual engaged in trash foraging at the accommodation perimeter, documenting active supply behaviour and the behavioural and ecological transition in high-tourism zones. These images provide direct visual evidence for correlation matrix findings (Figure 6), showing the negative relationship between natural foraging (FO) and active supply (AS; $r = -0.31$), linking behavioural change to altered ecosystem function. Photographs reproduced with permission from Ms. Janire Sánchez, 2022.

4.1.3. Agonistic

Agonistic behaviours among *Cebus imitator* serve to regulate intraspecific competition, particularly for resources. In the accommodation area, where provisioned food is readily available, increased joint threatening behaviour may reflect intensified competition for these high-value food resources [6].

Monkeys' behavioural responses to human disturbance are difficult to predict due to the numerous variables influencing their behaviour. In tourist areas, individuals may be more responsive due to frequent contact with humans, or less responsive if they are habituated. In contrast, monkeys with little prior human contact tend to react more intensely to occasional disturbances [7]. Regarding agonistic behaviour, although higher rates were observed at accommodation sites, the small sample size prevented these differences from reaching statistical significance. Anecdotally, individual threats toward the observer were recorded at the accommodation, suggesting that extreme habituation may cause these animals to lose fear of humans and even perceive them as potential food sources.

Therefore, based on our analysis, we can state that foraging is inversely correlated with "threatening" and "active supply" is positively correlated with "joint threatening". However, these relationships were not statistically significant, although a larger sample size would likely have allowed us to detect them. Capuchins, known for their cognitive flexibility and complex behavioural repertoire [15], may be particularly prone to developing habituated behaviours in response to repeated human contact.

Collectively, these three behavioural dimensions (locomotion, feeding, and agonistic patterns) suggest that tourist accommodation sites may exert greater anthropogenic pressure on Cebus imitator populations compared to the more strictly regulated Jaguar Trail. The behavioural suite observed (lower substrate use, increased use of anthropogenic foods, and higher—but not statistically significant—rates of agonistic interactions) is consistent with a population potentially moving toward greater habituation and dependence on human-derived resources, although our limited sample size and exploratory design preclude definitive conclusions. These findings raise critical conservation questions that extend far beyond the immediate welfare of individual primates at Tortuguero to encompass broader implications for primate populations throughout tourism-influenced landscapes worldwide. Understanding and managing these impacts thus requires examining not only individual behavioural responses but also the ecosystem-level consequences of altered primate ecology.

4.2. Implications for Conservation and Tourism Management and Future Work

Primates' habituation to human presence raises new risks and conservation challenges such as potential human–wildlife conflicts. In regions of long-term shared habitats, such as in parts of Asia, injuries to both humans and primates are common. Hutschenreiter [18] notes that such shared habitats can also increase animal mortality as a side effect of coexistence. Habitat fragmentation further affects infant survival [19], highlighting the importance of well-designed tourist infrastructure and the establishment of biological corridors. Furthermore, habitat loss remains the most significant threat to the survival of many primate species [20,21].

Similar studies in other regions, such as [22], report changes in feeding behaviour influenced by anthropogenic food when primates share habitats with humans. Tortuguero is attractive to ecotourists, organizations, and universities due to its unique natural characteristics. However, conservation efforts in the area have primarily focused on sea turtles, leaving mammals, including *Cebus imitator*, with less attention. Developing a diversified ecotourism plan—such as reopening the old Gavilan Trail as an interpretative hiking route—could both support conservation and promote sustainable economic opportunities.

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Conservation measures should also prioritize ecosystem restoration. Reforestation along the boundaries of hotels in direct contact with the forest, using plants from the *Anacardiaceae* and *Melastomataceae* families that *Cebus imitator* feed on, would help restore habitats [6]. Equally important is a clear wildlife management plan for tourists and staff that combines behavioural rules (no feeding, measures to prevent food theft, and reducing food access in restaurants and bars) with environmental education. Signage in the village, at Jaguar Trail access points and at key hotels can effectively raise visitor awareness and promote pro-conservation behaviour [23]. The community's current efforts to curb deliberate feeding already represent a meaningful step toward reducing conflict.

In a context where wildlife-based tourism is one of the fastest-growing industries in the world [7], additional strategies to mitigate human–wildlife conflicts are highly necessary. Although white-faced capuchins are not as threatening or aggressive as other primate species—such as the rhesus macaque (*Macaca mulatta*)—the possibility of translocating certain groups has been discussed in the broader primate-tourism literature. However, in Tortuguero we currently lack systematic data on population density, troop home ranges, and habitat availability within the park, which are essential prerequisites for evaluating any translocation programme. In this context, translocation should be regarded as a long-term, hypothesis-generating management option rather than an immediate recommendation, and future research would need to assess its ecological feasibility and social acceptability before any implementation is considered [21]. Other studies, such as [24], also highlight the potential of physical exclusion measures and non-invasive deterrents as effective tools to reduce negative interactions between humans and primates.

Finally, this experience in Tortuguero revealed a critical coordination gap between the community, accommodation providers, and conservation organizations. A gap that extends beyond wildlife management to encompass the broader sustainability of tourism development. Engaging impartial mediators to facilitate dialogue among stakeholders is essential to strengthen conservation efforts and ensure equitable benefits for both fauna and ecosystems. Evidence from comparable conservation-based tourism initiatives, such as those documented at Manuel Antonio National Park in Costa Rica, demonstrates that successful coexistence of wildlife conservation and ecotourism requires sustained institutional coordination and genuine community engagement [25]. The success of sea turtle conservation in Tortuguero demonstrates that effective wildlife conservation can coexist with ecotourism, supporting both biodiversity and local economic growth. This coordinated approach has proven effective in maintaining both biodiversity protection and sustainable livelihoods, suggesting that similar mechanisms in Tortuguero could address current management gaps and generate long-term conservation benefits. Such coordination represents not merely a conservation option but a prerequisite for the long-term ecological and economic sustainability of Tortuguero as a globally significant protected area.

4.3. Limitations and Caution in Interpretation

After interpreting the data, it is essential to recognize several limitations in the analysis. First, the limited temporal and spatial sampling effort constrains statistical power and broader inference. Extending monitoring over a longer period, ideally encompassing at least a full year, would allow greater ecological and social variability to be captured, including high and low tourist seasons, differences in resource availability, and a wider range of troops, thereby strengthening the robustness of temporal comparisons. Additionally, quantitative habitat metrics (e.g., canopy height or understory density) were not available for inclusion as covariates in the statistical models. Although habitat characteristics were qualitatively assessed during site selection, the absence of standardized measurements limits our ability to incorporate habitat variables into the statistical analysis. It is also impor-

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tant to acknowledge that correlation does not imply causation; although some behavioural variables frequently co-occurred within the same context, this does not necessarily indicate a direct or causal relationship, as these associations may be influenced by unmeasured variables or external environmental factors. Furthermore, while some behavioural differences between locations follow clear tendencies, not all results are statistically robust, which is reflected in several *p*-values that did not reach conventional significance thresholds ($p < 0.05$). Finally, because individual animals or troops could not be identified, we cannot rule out the possibility of pseudoreplication, as repeated sampling may violate assumptions of independence and potentially overestimate the precision of statistical analyses. However, the sampling design, distributed across multiple days and spatially separated by a river and distances exceeding typical daily movement ranges for the species, combined with the ecological characteristics of these wide-ranging wild animals, reduces—though does not eliminate—the likelihood of repeatedly observing the same individuals or groups across sites.

5. Conclusions

As a small-scale case study based on 261 min of focal observation, our findings must be interpreted with caution. Our preliminary findings show significant differences in locomotion patterns between the two sites, with low-substrate walking significantly reduced on the Jaguar Trail compared to accommodations ($p = 0.005$), providing strong support for Hypothesis H1.1. This behavioural shift is primarily explained by differential food availability: active food supply behaviour—direct consumption of anthropogenic foods from human sources—was observed exclusively in accommodation areas ($p = 0.070$), indicating that tourism infrastructure creates an environment where primates concentrate near human structures rather than dispersing into the forest canopy. Although ground foraging for natural fruits may also contribute to low substrate use, the strict absence of active food supply on the Jaguar Trail, combined with the negative correlation between foraging and active supply ($r = -0.31$), suggest that anthropogenic food availability may be an important driver of the observed locomotion shift, although other unmeasured factors (e.g., fine-scale habitat structure) could also contribute.

Field observations (June–October 2022) revealed that critical management interventions were absent at accommodation sites. Accessible food sources persisted, and primates exhibited active food provisioning behaviour exclusively in these areas, indicating inadequate food access controls. Based on these behavioural patterns and established conservation literature, we recommend immediate adoption of an evidence-based management protocol addressing these deficiencies through the following:

(1) Secured waste management and elevated food storage using wildlife-proof infrastructure and systematic waste segregation protocols [26]; (2) ranger-based monitoring and visible enforcement of existing wildlife feeding prohibitions, implementing structured patrol systems and documented data collection to improve compliance; and (3) targeted environmental education programs that interpret both individual animal welfare and ecosystem-level consequences of human–wildlife interactions, as research demonstrates situational environmental education significantly shifts tourist behaviour (standardized path coefficient = 0.78) toward conservation objectives [27]. These integrated interventions directly address the observable management gaps documented in our study and align with demonstrated best practices for ecotourism governance.

Our observations of active food supply at accommodation sites exemplify three interconnected conservation challenges in primate tourism: habituation, provisioning, and disease transmission. Habituation—the reduced flight response to humans—increases primate vulnerability to poaching and human–wildlife conflict, while provisioning actively

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generates negative outcomes including escalating aggression, intra-group competition, obesity, and metabolic disorders. Among these threats, zoonotic disease transmission—the direct transfer of human pathogens to wildlife through proximity and contact—represents one of the most critical and least manageable threats to long-term primate population viability [21]. These interconnected issues collectively demonstrate the need for evidence-based tourism practices that actively safeguard both wildlife populations and their essential habitats.

Costa Rica has constructed an international reputation as a leading nature-based tourism destination since the creation of its first protected areas in the 1960s [28,29], positioning itself as a "green exception" within Latin America. Today, the country's global image as an "exceptionally green" destination continues to attract ecotourists, organizations, and researchers worldwide. While this positioning has undoubtedly contributed positively to conservation financing and political support for habitat protection, it simultaneously creates significant ecological and social contradictions. Tourism expansion in protected areas can displace local communities, fragment habitats, and catalyse wildlife habituation—dynamics well-documented in comparative studies.

Most critically, tourist social imaginaries—deeply embedded cultural constructions such as the romantic association with "untouched tropical paradise," indigenous peoples existing in "natural harmony" with wildlife, and the symbolic ethos of "Pura Vida" (literally "pure life")—powerfully shape visitor expectations and behaviours [30,31]. These imaginaries frequently result in harmful practices as tourists attempt to secure "authentic" wildlife experiences at any cost, including violating wildlife feeding prohibitions and disturbing critical habitats. Addressing these contradictions requires integrating social, political, and cultural dimensions into conservation strategies [32], moving beyond purely ecological or economic approaches. The present study—demonstrating that primates in high-tourism areas exhibit reduced natural foraging, increased anthropogenic food dependence, and elevated agonistic behaviours—provides empirical evidence of how social imaginaries translate directly into ecological degradation.

Effective conservation in protected areas demands integrated approaches transcending purely economic or biological frameworks. Social, political, and cultural dimensions must be systematically integrated into conservation strategies, as tourism expansion creates complex human–wildlife interactions unmanageable through habitat protection alone. To sustain both Costa Rica's conservation leadership and long-term ecological integrity, we recommend urgently implementing the following: (1) evidence-based management protocols addressing food access restrictions and enforcement of wildlife feeding prohibitions; (2) targeted environmental education for tourists, hospitality staff, and local communities; and (3) meaningful stakeholder participation ensuring equitable benefits for indigenous and Afro-Caribbean communities, historically dependent on these ecosystems. Without coordinated, integrated action, Costa Rica risks compromising both its conservation credibility and the ecological functions underlying sustainable tourism viability.

Future research should extend monitoring across full annual cycles, include a larger number of troops per site, incorporate quantitative habitat metrics as covariates, and adopt designs that explicitly track individually identified primates. Such work would allow rigorous tests of the hypotheses generated here regarding locomotion shifts, diet supplementation, and emerging agonistic patterns under contrasting ecotourism pressures.

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Strategies for Coordinated Development Between Local Communities and the Northeast China Tiger and Leopard National Park: Case Study of the Hunchun Area

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Abstract: As an important component of China's conservation strategy, the Northeast China Tiger and Leopard National Park faces conflicts between environmental protection and community development. Taking the Hunchun area as a case study, here a choice experiment is employed to construct a policy-scenario model encompassing participation mechanisms, benefit-sharing models, and industrial development. Our analysis of farmers' heterogeneous policy preferences reveals the following. (1) Farmers significantly prefer cooperative organization participation, ecological industry, and ecological compensation while showing less acceptance of agricultural deep processing. (2) Heterogeneity analysis indicates that middle-aged, educated, and low-income male farmers have stronger preferences for policy optimization. (3) Existing homogeneous policies do not satisfy diversified stakeholder demands. We propose a governance framework integrating ecology, industry, and institutions, suggesting practical pathways such as optimizing interest distribution mechanisms, innovating green industry models, and establishing cross-regional ecological compensation mechanisms. This study provides theoretical and practical support for reconciling conservation and development in protected areas.

Keywords: Northeast China Tiger and Leopard National Park; coordinated community development; choice experiment method; policy preferences

1. Introduction

National parks, recognized as critical for conservation, have unique institutional value for supporting ecological security and coordinating community development. China initiated its national park pilot program in 2015, based on the principles of "ecological conservation as the primary objective, national representativeness, and public accessibility". However, there is always competition between ecological conservation and community development. Communities adjacent to and close to national parks often disproportionately bear the external costs of environmental protection, while receiving insufficient compensation, resulting in imbalances between rights, responsibilities, and benefits compared to more distant communities. Such imbalances constrain the sustainable development of protected areas [1].

Related research has largely focused on three dimensions. First, cost-compensation: researchers have advocated internalizing conservation costs by creating ecological jobs and transferring ecological payments [2,3]. Second, industrial substitution pathways explore

alternative livelihoods such as ecotourism and green agricultural product certification [4,5]. Third, multi-stakeholder governance mechanisms involving government, enterprises, and communities [6]. While such studies are important references for policy design, they generally lack empirical investigations of behavioral preferences, resulting in structural discrepancies between policy provisions and farmers' demands.

As one of China's first pilot national parks, the Northeast China Tiger and Leopard National Park exhibits a distinctive ecology–economy duality in the Hunchun region: it is a habitat for endangered species and traditionally produces specialty agricultural products such as Yanbian cattle. Local governments have implemented various policies to mitigate the conservation–development conflict arising from park establishment. Take Yanbian cattle breeding as an example (According to data statistics, there will be a total of 1832 Yanbian yellow cattle breeders in Hunchun City in 2023, including 1758 free-range breeders and 74 large-scale breeding farms), through implementing the "cattle relocation" initiative in the "Jilin Province Regulations on Mountain Closure and Grazing Ban Management", free-range cattle have been completely removed from the park. The government has also had leading agricultural enterprises establish beef cattle breeding demonstration bases outside the park through public–private partnerships. This industrial relocation model initially coordinated development between ecological conservation and industrial transformation. However, as the national park transitions from intensive construction to standardized management, the sustainability of existing policies faces challenges. The original ecological compensation mechanism, which primarily relies on financial transfers, struggles to meet local residents' growing demand for livelihood development. Especially with the aging of local farmers and the increasing degree of rural hollowing out, farmers lack the motivation to develop their own industries, and due to physical reasons, can only engage in low-value-added labor during the production cycle of crops.

More critically, the current policy framework inadequately addresses the structural contradictions between conservation and development. As the park transitions from emergency management to normalized governance, the original compensation mechanism centered on "ecological compensation + industrial substitution" does not adequately address the endogenous development needs of local communities. This contradiction is particularly evident in the incompatibility between current compensation standards and the actual costs of industrial transformation, as well as the structural imbalance between government-led compensation inputs and market-oriented development mechanisms. Future policies should aim to establish a diversified compensation mechanism that integrates government guidance, the market, and community participation. This system should focus on ecological product value realization, aiming to enhance the sustainability of industrial development and community participation.

Existing research on coordination between protected areas and local communities overlooks two critical dimensions: (1) the heterogeneous preferences of stakeholders regarding policy combinations; and (2) participatory governance logic in institutional design. The choice experiment method offers advantages in this context, as it simulates policy scenarios to reveal stakeholders' trade-off mechanisms between ecological conservation and economic development [7]. This approach provides a novel methodological perspective for addressing the current mismatch between policy supply and demand.

Focusing on the Hunchun pilot zone, this study develops a choice experiment model incorporating participation mechanisms, benefit-sharing mechanisms, policy support, and industrial models. Specifically, we examine (1) the core demands of local communities regarding coordinated development policies; (2) heterogeneity in preferences across different demographic groups; and (3) optimal policy combinations. By revealing the causal mechanisms between policy attributes and community preferences, this study constructs

a participatory governance framework grounded in empirical evidence, thereby offering theoretical and practical insights for optimizing the design of conservation and development policies.

2. Materials and Methods

2.1. Study Area and Data Source

The Hunchun area of the Northeast China Tiger and Leopard National Park is located on China's northeastern border. In recent years, the number of Manchurian tigers appearing in this area has increased annually. In addition to solitary tigers, female tigers have been breeding in this reserve for a long time. Geographically, the Hunchun area serves as an ecological corridor for the free migration of Manchurian tigers, Amur leopards, and their prey species. It is also a strategic passage for Manchurian tigers migrating from Russia to inland China [8].

We selected the farmer households surveyed in this study using multistage stratified random sampling. Considering the actual situation of the communities surrounding the Hunchun area, we selected 51 villages, including 5 from Mijiang Township, 6 from Yangpao Manchu Township, 6 from Banshi Town, 15 from Hadamen Township, and 19 from Chunhua Town (Figure 1). About 10 farmer households were randomly selected from each village based on their household registration for the survey, resulting in 534 farmer household questionnaires collected. All farmer households surveyed resided in the study area for an extended period.

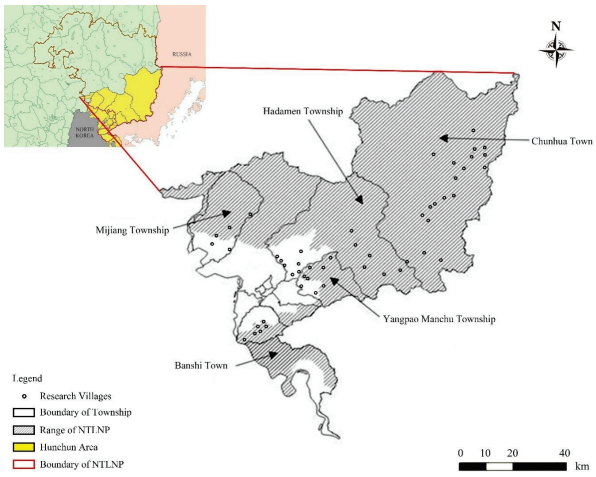

Figure 1. Schematic diagram of the Hunchun area of the Northeast China Tiger and Leopard National Park.

2.2. Research Hypotheses

Utility, a central concept in consumer behavior theory, denotes the degree of satisfaction a consumer derives from consumption choices or needs fulfillment, serving as a behavioral and decisional foundation [9]. Functionally, utility reflects decision-makers' subjective psychological evaluations of outcomes associated with alternative choices. Empirical studies have demonstrated that farmers' policy preferences are an important basis for coordinating conservation areas with adjacent communities [10]. Notably, heterogeneity in individual characteristics, livelihood capital, and personal preferences among farmers leads to significant variations in policy demands, adaptability, and participation levels. Studies have examined rural households' evaluations of policies implemented by reserve administrations or local governments, encompassing areas such as policy determinants [11], satisfaction levels [12], and cost–benefit analysis [13]. Methodologically, these investigations often use case studies, game-theoretic analyses, and cost–benefit approaches. As

a robust stated preference technique, the choice experiment method enables the precise measurement of the marginal value derived from attribute variations in alternative policy packages. This approach can facilitate the estimation of welfare effects attributable to specific policy attribute enhancements by analyzing farmers' selections among policy bundles with varying attributes.

Based on utility theory, rural household decisions maximize utility. Consequently, variations in attribute levels across policy alternatives change household preferences and their feasible choice sets. To investigate rural households' developmental needs and expectations, we designed multiple policy bundles, differentiated by policy objectives and technical attributes. These bundle options provide households with the best choice for their specific circumstances, indicating the policy design that best addresses their demands. Respondents selected their preferred option from multiple simulated choice scenarios. Analyzing the selection patterns of households in communities adjacent to the Northeast China Tiger and Leopard National Park allows us to quantify the marginal welfare contributions of distinct policy attributes. Each respondent's aggregate welfare valuation is based on multiple attributes, with households consistently prioritizing utility maximization. Using variations in choice set configurations, this framework reveals attribute-specific preference intensities, and how policy attribute adjustments influence rural welfare outcomes.

To investigate how governments can facilitate diversified industrial development among rural households while ensuring community well-being under protected area policy constraints, we propose the following hypotheses based on random utility theory.

H1. *Rural households exhibit a systematic preference for choice sets delivering higher utility.*

H2. *Individual characteristics (specifically, age, gender, educational attainment, and annual household income) have an impact on whether a family will make choice strategies.*

3. Experimental Design

This section outlines the methodological framework adopted for evaluating stakeholder preferences and policy effectiveness. The study employs choice experiments, a robust approach for simulating real-world decision-making scenarios, to identify key factors influencing the adoption of sustainable economic development policies. The design process involves constructing choice sets, defining policy attributes, and analyzing combinations to assess trade-offs and priorities.

3.1. Design of Choice Sets and Setting of Alternative Attributes

The foundation of choice experiments lies in systematically defining policy alternatives and their attributes to reflect real-world decision contexts. This subsection details the process of attribute selection, level assignment, and combinatorial logic used to generate choice scenarios. The rigorous design ensures that the experiment captures meaningful variations in policy configurations while minimizing cognitive overload for participants.

3.1.1. Design of Choice Sets

Choice experiments require clearly defining the various attributes of different alternatives and their corresponding levels and, on that basis, constructing suitable choice scenarios or choice sets. "Local support policies" refer to a series of measures, actions, and related requirements involved in promoting local economic development to achieve sustainable economic development in a region. Based on the actual situation of livelihood activities of farmers in the Hunchun area of Northeast Tiger and Leopard National Park, and combined with the needs of economic development, we divide the attributes of local

sustainable economic development policies (alternative solutions) into four categories: participation channels, benefit methods, policy support, and industrial models, which are used to describe the participation methods of local farmers in livelihood activities, the ways in which agricultural products obtain income, local support policies for farmers' livelihoods, and feasible paths for agricultural industry development. Based on these attributes, it is possible to comprehensively measure the livelihood behavior of local farmers. Table 1 shows a collection of all possible combinations that contain these attributes. Table 2 shows an example of a questionnaire selection set.

Table 1. Attribute levels and descriptions.

Attributes	Levels	Attribute Descriptions
Participation Channels	Direct Farmer Participation Farmer + Cooperative Partnership Farmers + Leading Enterprise Participation	Production Engagement Pathways for Farmer-Generated Agricultural Products
Marketing Models	Direct Farm-to-Consumer Sales Contract Farming Lease-Back Farming Model Equity-Based Cooperative Farm	Marketing Frameworks for Smallholder-Generated Agri-Produce
Policy Support	Core Subsidy Programs Niche Agricultural Sector Incentives Agri-Financial Inclusion Mechanisms Concessional Licensing Schemes	Tiered Government Support Mechanisms for Smallholder-Centric Agricultural Development
Agri-Industrial Frameworks	Integrated Crop–Animal Systems Value-Chain Deep Processing Integration Agro-Ecotourism Experience Packages	Structural Ecosystem of Agrarian Economic Models for Farming Households

Table 2. Example of questionnaire selection set.

Selection Set	Plan1	Plan2	Plan3	Plan4 (Current Situation)
Participation Channels	Farmer + Cooperative Partnership	Direct Farmer Participation	Direct Farmer Participation	Direct Farmer Participation
Marketing Models	Lease-Back Farming Model	Lease-Back Farming Model	Direct Farm-to-Consumer Sales	Direct Farm-to-Consumer Sales
Policy Support	Core Subsidy Programs	Agri-Financial Inclusion Mechanisms	Niche Agricultural Sector Incentives	Core Subsidy Programs
Agri-Industrial Frameworks	Value-Chain Deep Processing Integration	Agro-Ecotourism Experience Packages	Agro-Ecotourism Experience Packages	Integrated Crop–Animal Systems
Your Choice				

3.1.2. Setting of Alternative Attributes

This subsection elaborates on the specific attributes and levels used to define the policy alternatives in the choice sets. Each attribute is carefully selected to capture key dimensions of local sustainable economic development, ensuring that the study reflects the diverse needs and priorities of stakeholders.

1. Participation Channels

Farmers participate in agricultural production in various ways. Based on the requirements of the "National Agricultural Sustainable Development Plan (2015–2030)", which aimed to establish mechanisms conducive to sustainable agricultural development, and considering the actual situation of the Hunchun area, we designed three different options: "farmers participating directly" (as the current baseline option), "Farmer + cooperative participation", and "farmers + leading enterprise participation".

As an organizational form of community production and management, cooperatives unite farmers with similar needs or wishes to facilitate joint production and management. The cooperative model combines the enthusiasm of family farm management with the advantages of scale. Participation in cooperatives is a way for farmers to participate in collective community decision-making. By giving up some of their own freedom and paying certain transaction costs, farmers cooperate to complete tasks, including production, processing, sales, and purchases. Researchers generally believe that cooperatives can help achieve agricultural industrialization [14], alleviate poverty [15], and promote rural revitalization [16].

Leading enterprises refer to enterprises that focus on the production, processing, or circulation of agricultural products, meet the prescribed standards in terms of scale and operational indicators, and have been recognized by relevant government departments. Leading enterprises are the pillars of the modern agricultural industrial system, effectively promoting rural revitalization, agricultural modernization, and farmers' income and employment. Notably, leading enterprises increase farmers' income while driving their employment and the development of agricultural processing [17]. Meanwhile, as top enterprises in the industry, they can also accelerate the gathering of innovative elements and build mature innovation networks and ecological elements. Leading enterprises can support the development of local characteristic industries, promote the integration of enterprises with local production factors, and achieve the innovative transformation and development of local characteristic industries [18].

2. Sales Model

Most farmers in the communities surrounding the Hunchun area of the Northeast China Tiger and Leopard National Park generate income through self-production and self-marketing, directly connecting with consumers in the market. This method is relatively primitive, requiring farmers to conduct production, processing, transportation, and sales on their own. The organizational level, scale, and professionalism of this method are relatively low, while the mobility, randomness, and volatility of the transaction mode are high. Additionally, since farmers operate and sell independently, it is difficult for them to form stable sales relationships, and the level of trust between consumers and farmers remains low [19].

Contract farming, also known as agreement farming, centers on the production and supply of agricultural products based on contracts signed by both parties. The essence of this model is that producers provide specific types and quantities of agricultural products at agreed times and prices according to the actual needs of buyers, thereby achieving precise matching between supply and demand [20]. Through contract farming, farmers can effectively reduce the price risks they face and ensure income stability. At the same time, companies providing contracts to farmers can reduce uncertainty in the agricultural product acquisition process, guarantee a stable source of production materials, and thus better plan production and supply chain management.

As a land circulation model spontaneously explored by farmers, the reverse leasing and subcontracting mechanism operates as follows. The community collective (or village collective) first takes back the land originally contracted to farmers, conducts unified management and planning, and then re-contracts these lands in a contiguous form to

farmers to support their agricultural production activities [21]. Compared with the ordinary land transfer, contracting, and leasing activities spontaneously formed by farmers, reverse leasing and subcontracting can more stably concentrate management rights for contiguous land and ensure that there are no property rights issues during the land circulation process. Through unified planning and management by the community collective, reverse leasing and subcontracting can fully leverage the advantages of scale operations, thereby enhancing economic benefits.

As a new agricultural management model, shareholding cooperative farms can further rejuvenate rural economies. Given its shareholding cooperative characteristics, the shareholding cooperative farm, which possesses stronger institutional features, is an ideal model for agricultural industrialization and modernization. It transforms the village collective economic organization into a substantive agricultural production and operation entity, fully leveraging the institutional advantages of "political–social integration and organizational unity" and helping enhance the level of organization and scale in agricultural production [22].

3. Policy Support

The phrase "agricultural support policies" refers to the support provided by the government to farmers aimed at increasing their income or reducing production costs. Because agricultural production is cyclical and vulnerable [23], investment returns are lower than in other industries. To ensure agricultural security and maintain the industry, policies that guarantee higher-quality agricultural development need to be implemented. Currently, in the Hunchun area, major agricultural support policies include subsidies for grain cultivation, quality seeds, agricultural machinery, and the scrapping and renewal of agricultural machinery.

As agricultural industrialization diversifies, universal support policies will not meet development needs. The Hunchun beef cattle breeding industry needs a more complete social service system to support high participation and penetration upstream and downstream of the industrial chain. This requires more targeted preferential industrial subsidy policies from government departments to compensate agricultural operator losses due to constraints and to ensure their production and operation.

Agricultural financial support policies are designed to promote agricultural economic development in China. Agricultural financial policies focus more on safeguarding local agricultural development than general financial support policies, and serve the local agricultural economy rather than purely pursuing profits. Their main goal is to promote healthy agricultural development by providing stable, reliable financial support for agriculture. Therefore, these policies have stronger social and political characteristics, reflecting local governments' support and assistance for the agricultural economy [24].

According to the International Franchise Association, franchising is a business model centered on a contractual partnership between a franchisor and a franchisee. In this model, the franchisor grants the franchisee the right to use its name, trademark, technology, products, and other resources for commercial activities in return for compensation. This business model achieves mutual benefit and win-win results for both parties through shared brands, technology, and resources [25].

4. Industrial Models

Agricultural production in the Hunchun area mainly includes food crop cultivation, economic crop cultivation, and beef cattle breeding. Community farmers often adopt a combination of planting and breeding to sustain their livelihoods. The main cultivated food crops are corn, rice, and soybeans. Economic crops include apple trees and Auricularia (wood ear mushrooms), among others. The breeds raised are chiefly local specialty beef

cattle and hybrid beef cattle varieties. Typically, farmers who cultivate food crops store straw and other harvested residues as food sources for beef cattle in the winter. At the same time, they collect manure from beef cattle to return to the fields as a natural fertilizer for the next planting season.

Deep processing of agricultural products refers to the multiple and complex processing of agricultural products, transforming them from primary products into final products with higher added value, finer quality, wider applications, and longer shelf life. The deep processing of agricultural products involves using scientific processing to ensure product quality and meet market demands. The deep processing of food crops, economic crops, and livestock breeds is the most value-added segment of the agricultural product industry chain. In addition to addressing issues of periodic surplus in grain supply, the deep processing of agricultural products can effectively promote the full utilization of grain resources and increase farmers' production and income [26]. This will help increase the added value of agricultural products, promote locally clustered grain cultivation, and enhance farmers' production and income.

Ecotourism has become an important way for people to get close to and appreciate nature, representing a significant trend in tourism development. Through ecotourism, people can experience the charm of nature and promote the awareness of harmonious coexistence between humans and nature. Different from general tourism, ecotourism emphasizes environmental protection as a prerequisite. By allowing tourists to experience and understand the environment, it provides environmental education to tourists, enabling them to gain different tourism experiences [27].

3.2. Ensuring the Validity of the Experiment

To increase experimental reliability, the choice sets must be reasonable, and the choices must be as realistic as possible. Thus, during the interviews with farmers, we introduced the main purpose of the experiment and briefly explained the choice method: "During this survey, you will be given a series of questions, with four options to choose from. Options 1, 2, and 3 are combinations of governmental development policies, and option 4 is the existing policy. You are asked to select your most preferred option". Afterward, we presented the farmers with five different choice sets. If the farmers had difficulty understanding any questions, we further explained them to ensure the validity of the experimental data.

3.3. Variable Definitions and Descriptive Statistics

In the model constructed here, the dependent variable is whether a particular scheme is selected by farmers. If a scheme is selected, it is assigned a value of 1; if it is not selected, it is assigned a value of 0. The ASC (alternative-specific constant) represents farmers choosing an "improved scheme", which means that in each choice set, a value of 1 is assigned when farmers choose schemes ①, ②, or ③, and a value of 0 is assigned when they choose scheme ④. The core explanatory variable in the model is the attributes specifically, whether the scheme is selected by farmers. To further explore potential sources of heterogeneity in farmers' preferences for government agricultural support policies, the individual characteristic variables of farmers (including age, gender, education, and income) and location characteristics (e.g., whether the area is within the boundaries of the national park) are included in Equations (5) and (6), respectively. Table 3 shows the definitions and descriptive statistics of the variables.

Table 3. Variable Definitions and Descriptive Statistics.

Variable	Definition and Assignment	Mean	Std. Err.
Dependent Variable			
Whether the Plan is Selected	Selected = 1, Not = 0	0.2500	0.0042
ASC	Selected ①, ②, ③ = 1, Not = 0	0.7500	0.0042
Attributes and Levels			
Participation Channels			
Direct Farmer Participation	Yes = 1, No = 0	0.6000	0.0047
Farmer + Cooperative Partnership	Yes = 1, No = 0	0.2000	0.0039
Farmers + Leading Enterprise Participation	Yes = 1, No = 0	0.2000	0.0039
Marketing Models			
Direct Farm-to-Consumer Sales	Yes = 1, No = 0	0.4000	0.0047
Contract Farming	Yes = 1, No = 0	0.2000	0.0039
Lease-Back Farming Model	Yes = 1, No = 0	0.2000	0.0039
Equity-Based Cooperative Farm	Yes = 1, No = 0	0.2000	0.0039
Policy Support			
Core Subsidy Programs	Yes = 1, No = 0	0.4000	0.0047
Niche Agricultural Sector Incentives	Yes = 1, No = 0	0.2000	0.0039
Agri-Financial Inclusion Mechanisms	Yes = 1, No = 0	0.2000	0.0039
Concessional Licensing Schemes	Yes = 1, No = 0	0.2000	0.0039
Agri-Industrial Frameworks			
Integrated Crop–Animal Systems	Yes = 1, No = 0	0.6000	0.0047
Value-Chain Deep Processing Integration	Yes = 1, No = 0	0.2000	0.0039
Agro-Ecotourism Experience Packages	Yes = 1, No = 0	0.2000	0.0039
Individual Characteristics			
Gender	Woman = 0, Man = 1	0.7734	0.0047
Age	Actual age	58.67	0.0926
Education Level	Primary school and below = 1, junior high school = 2, secondary vocational school or high school = 3, junior college or bachelor's degree and above = 4	1.9906	0.0137
Annual Income	Logarithm of total annual household income (yuan)	10.8985	0.0112

Note: The total number of observations for the explained variable and scheme attribute variables is 10,680; the total number of observations for the individual farmer characteristic variables is 534.

4. Model

Grounded in theoretical foundation analysis and behavioral choice analysis, choice experiments construct multiple scenarios with varying attribute combinations for respondents to evaluate and select. This approach enables researchers to gain deeper insights into respondents' decision-making processes and preference orientations during multi-alternative selections [28]. The choice set–centric questionnaire design requires respondents to engage in higher cognitive processing when making trade-offs, thereby enhancing participants' engagement and depth of contemplation. This design significantly improves the precision of behavioral observation and data recording. Furthermore, in agricultural household research, choice experiments demonstrate incentive compatibility advantages that effectively stimulate respondent motivation [29,30], thereby ensuring the scientific validity and empirical reliability of the research outcomes.

Based on Lancaster's attribute value theory and McFadden's random utility theory, we construct a behavioral analysis framework for agricultural households. The utility (U)

for decision-maker i (i.e., the surrounding communities in the Northeast China Tiger and Leopard National Park) when selecting policy combination j can be expressed as

$$U_{ij} = V_{ij} + \varepsilon_{ij}. \quad (1)$$

In Equation (1), V_{ij} represents the observable utility component for farmers in the surrounding communities, which can be explained by the attributes of alternative j. ε_{ij} represents the random disturbance term; that is, the unobservable utility component for farmers in the surrounding communities.

Based on the principle of utility maximization, the probability that a farmer (decision-maker i) in the surrounding communities of the area will choose a particular alternative from a set of alternatives (also known as a choice scenario) C is

$$P_{ig} = \text{Prob}(U_{ig} > U_{ih}) = \text{Prob}\left[(V_{ig} + \varepsilon_{ig}) > (V_{ih} + \varepsilon_{ih})\right]; \forall h \neq g; g, h \in C. \quad (2)$$

When ε_{ig} in Equation (2) strictly follows an extreme value distribution, is independently and identically distributed, and satisfies the independence of irrelevant alternatives assumption. Equation (2) represents a multinomial logit model. Although the multinomial logit model presumes consistent choice preferences for decision-maker i, in reality, owing to individual differences among farmers, their preferences and demands for various policy objectives exhibit heterogeneity. In such cases, this restrictive assumption of the multinomial logit model does not align with reality [31]. Therefore, by allowing randomness in the involvement of attributes to relax the assumption, Equation (2) becomes a random parameters logit model.

In practical analysis, the observable utility V_{ij} in the aforementioned Equations (1) and (2) are typically defined in a linear form representing the specific attributes of the alternatives:

$$V_{ij} = \alpha_{ASC} ASC_i + \sum_{k=1}^{K} \beta_k X_{ijk}. \quad (3)$$

In Equation (3), ASC_i represents the alternative-specific constant for the choice, and its coefficient α_{ASC} signifies the average utility derived from unobservable moral factors influencing a farmer's choice of a specific alternative. When farmers choose any "policy adjustment" alternative within each choice set, ASC_i is assigned a value of 1; if farmers choose the "status quo" alternative, ASC_i is assigned a value of 0; X_{ijk} represents the k-th attribute variable of alternative j chosen by farmer i as the decision-maker, where β_k denotes the parameter to be estimated and K indicates the number of attributes for the alternatives.

In the random parameters logit model, the linear form of the observable utility V_{ij} can be expressed as

$$V_{ij} = (\alpha_{ASC} \pm \sigma_i) ASC_i + \sum_{k=1}^{K} (\beta_k \pm \delta_{ik}) X_{ijk}. \quad (4)$$

In Equation (4), σ_i represents the difference (i.e., standard deviation) between the individual coefficient of decision-maker i for their chosen alternative-specific constant (ASC_i) and the population mean coefficient α_{ASC}. If σ_i is significant, it indicates that there is heterogeneity in farmers' preferences for a specific policy combination alternative (the chosen alternative). Similarly, δ_{ik} represents the difference (i.e., standard deviation) between the individual coefficient of decision-maker i for the k-th attribute variable X_{ijk} and the population mean coefficient β_k. If δ_{ik} is significant, it suggests that there is heterogeneity in farmers' preferences for the k-th attribute when choosing from among policy alternatives.

To further investigate the sources of heterogeneity in farmers' preferences for policy alternatives, drawing on the literature [32], the observable utility V_{ij} in the random parameters logit model can be further expanded into two specific forms, as shown in Equations (5) and (6):

$$V_{ij} = (\alpha_{ASC} \pm \sigma_i)ASC_i + \sum_{k=1}^{K} (\beta_k \pm \delta_{ik})X_{ijk} + \sum_{m=1}^{M} \lambda_m (ASC_i \times Z_{im}). \quad (5)$$

$$V_{ij} = (\alpha_{ASC} \pm \sigma_i)ASC_i + \sum_{k=1}^{K} (\beta_k \pm \delta_{ik})X_{ijk} + \sum_{m=1}^{M} \gamma_m \left(X_{ijk} \times Z_{im}\right). \quad (6)$$

In Equation (5), $ASC_i \times Z_{im}$ represents the interaction term between the ASC_i and the individual characteristic variable Z_{im} of the farmer. This term is used to examine the sources of heterogeneity in farmers' preferences for a specific policy combination alternative (i.e., the alternative chosen by the farmer). Here, λ_m denotes the parameter to be estimated for the interaction term, and M represents the number of individual characteristic variables for farmers in the surrounding communities. Similarly, in Equation (6), $X_{ijk} \times Z_{im}$ represents the interaction term between the k-th attribute variable X_{ijk} and the individual characteristic variable Z_{im} of the farmer. This term is used to examine the sources of heterogeneity in farmers' preferences for the k-th attribute when choosing from among policy alternatives. Here, γ_m denotes the parameter to be estimated for the interaction term.

5. Results

The model is simulated using Stata 15.0. In the choice experiment, respondents were presented with five choice scenarios, each containing four alternatives. The total sample size for model estimation is 10,680 (534 individuals * 4 alternatives * 5 scenarios).

5.1. Farmers' Preferences for Agricultural Support Policies

First, we consider only the alternative-specific variables and the ASC in the multinomial logit model estimation of Equation (3). Table 3 shows the estimation results. The regression results indicate that "contract farming" in the sales model and "deep processing of the industrial chain" in the industrial development model are not significant. "Reverse leasing and subcontracting" in the sales model and "agricultural financial support" in policy support are significant at the 5% level while "ecotourism experience" in the industrial model is significant at the 10% level. All other policy attribute variables are significant at the 1% level, and the signs of their coefficients are positive.

ASC is significant at the 1% level with a positive coefficient. Based on the definition of ASC given earlier, this means that combinations of agricultural support policies can significantly increase actual utility for farmers in communities around the Northeast China Tiger and Leopard National Park. Compared with choosing the "maintain the status quo" alternative (i.e., alternative ④), respondents were more likely to accept combinations of agricultural support policies (i.e., alternatives ①, ②, and ③). This suggests that introducing different agricultural support policies among various alternatives can increase the actual utility for farmers in choosing to participate in these programs. Therefore, the support policy alternatives discussed in this study exhibit good utility trade-off characteristics, and the design of their attributes meets the technical application requirements of the choice experiment method, providing a strong guarantee for the accuracy and validity of the results.

From the estimation results regarding farmers' preferences for different policy attribute variables, in addition to "reverse leasing and subcontracting" in the sales model being significant at the 5% level (coefficient = 0.0198), variables such as "farmer + cooperative participation" and "farmers + leading enterprise participation" in the participation path-

ways, "shareholding cooperative farms" in the sales model, "specialty industry subsidies" and "franchise support" in policy support, and "ecotourism experience" in the industrial model are all significant at the 1% level (coefficients are 1.2322, 0.4130, 0.3454, 1.0908, 0.3726, and 0.0651, respectively). This indicates that changing existing participation pathways, adding more sales models, and expanding the scope of government support policies can all affect the utility farmers derive from choosing combinations of economic development support policies. Therefore, these policies can increase the likelihood of farmers choosing "improved alternatives".

It is also worth noting that compared with other improved alternative attribute levels, "deep processing of the industrial chain" is not significant while "ecotourism experience" is significant at the 1% level. This suggests that compared with developing ecotourism, developing deep processing has relatively lower utility for local farmers and does not significantly affect their likelihood of choosing "improved alternatives".

5.2. Effect of Farmer Heterogeneity on Preferences for Agricultural Support Policies

To further explore the sources of heterogeneity in farmers' preferences for policy combinations in communities around the Northeast China Tiger and Leopard National Park, we incorporate individual farmer characteristics into the model and perform maximum likelihood estimation using Equations (5) and (6). Table 4 shows the estimation results. Compared with the results without incorporating individual farmer characteristics, the coefficient signs and significance of the attribute variables do not change significantly. This indicates that the model results are highly robust, and the regression results after introducing interaction terms have stronger explanatory power, providing a more accurate, in-depth perspective.

Table 4. Farmer Program Attribute Preferences.

Variable	Coef.	Std. Err.
ASC	0.7068 ***	0.1329
Farmer + Cooperative Partnership	1.2322 ***	0.0642
Farmers + Leading Enterprise Participation	0.4130 ***	0.0694
Contract Farming	0.0247	0.0767
Lease-Back Farming Model	0.0198 **	0.0808
Equity-Based Cooperative Farm	0.3454 ***	0.0847
Niche Agricultural Sector Incentives	1.0908 ***	0.0864
Agri-Financial Inclusion Mechanisms	0.2453 **	0.0955
Concessional Licensing Schemes	0.3726 ***	0.0894
Value-Chain Deep Processing Integration	−0.0904	0.0701
Agro-Ecotourism Experience Packages	0.0651 ***	0.0695
Constant	−1.9323 ***	0.1246
R^2	0.0527	
Observations	10,680	

Note: *** and ** indicate significance at the 1% and 5% levels, respectively.

Specifically, Table 5 shows the estimation results for the interaction terms between farmers' age, gender, and education level and their respective ASCs. The results are significant at the 1% level, with positive coefficients. This suggests that as age and education level increase, farmers derive higher utility from "improved policies", and male respondents obtain higher utility than female respondents. The result for the interaction term between annual household income and ASC is also significant at the 1% level, but its coefficient is negative, indicating that annual income has a negative effect on farmers' utility. That is, farmers with lower annual incomes can obtain higher utility from "improved policies". Regarding the sample area, local low-income households typically adopt self-sufficient agri-

cultural planting models, making it difficult to achieve economies of scale and necessitating government policy support for sustainable economic growth. The alternative explanation is that farmers with higher annual incomes can obtain lower utility from "improved policies", meaning that the current situation has already enabled them to earn higher incomes, and therefore they are unwilling to choose to change. Farmers with more education have a higher degree of recognition of government support policies, which increases the actual utility derived from these policies. Therefore, male farmers who are old, have more education, and have relatively lower incomes are more willing to participate in the improvement of economic support policies.

Table 5. Heterogeneous Farmer Program Attribute Preferences.

Variable	Coef.	Std. Err.
ASC	1.3942 ***	0.4108
Farmer + Cooperative Partnership	1.2322 ***	0.0642
Farmers + Leading Enterprise Participation	0.4130 ***	0.0694
Contract Farming	0.0247	0.0767
Lease-Back Farming Model	0.0198 **	0.0808
Equity-Based Cooperative Farm	0.3454 ***	0.0847
Niche Agricultural Sector Incentives	1.0908 ***	0.0864
Agri-Financial Inclusion Mechanisms	0.2453 **	0.0955
Concessional Licensing Schemes	0.3726 ***	0.0894
Value-Chain Deep Processing Integration	−0.0903	0.0701
Agro-Ecotourism Experience Packages	0.0651 **	0.0695
Interaction Term		
ASC * Age	0.0449 ***	0.0057
ASC * Gender	0.1981 ***	0.0957
ASC * Education Level	0.2632***	0.0500
ASC * Annual Income	−0.3337 ***	0.0434
Constant	−1.9323 ***	0.1246
R^2	0.0718	
Observations	10,680	

Note: *** and ** indicate significance at the 1% and 5% levels, respectively.

6. Discussion

This study reveals the multidimensional mechanism of action underpinning coordinated development policies in national park communities. Regarding policy instruments, combined support policies have enhanced farmers' flexibility in responding to policies by reducing transaction costs and restructuring property rights relationships. Farmers are willing to alter their existing production participation approaches, diversify sales models, and obtain more policy support to improve their own utility. Meanwhile, agricultural deep processing does not significantly enhance farmers' utility, and farmers prefer to develop local ecotourism. After incorporating farmers' individual characteristics, we find that older farmers with more education derive higher utility from "improved policies". Additionally, farmers with lower annual incomes can obtain higher utility from different combinations of policy enhancements.

Cooperatives and leading enterprises, serving as pillars of community management and agricultural modernization, respectively, both have positive effects on stabilizing farmers' incomes and local employment [33,34]. Cooperatives reduce market transaction costs through embedded relational networks while leading enterprises build stable value chains through contractual relationships. Our choice experiment results also validate this point. Local farmers need to adopt more formal, well-established production and management organizations to realize the value of their products. This not only promotes

the more efficient utilization of local resources but also contributes to advancing local agricultural modernization. Ultimately, coordinated development forms a symbiotic model of "cooperatives addressing market failures–enterprises overcoming scale bottlenecks".

The sales methods of local agricultural product markets also need effective expansion. Integrating various agricultural product sales models can help farmers enhance the sustainability of their livelihood capital accumulation [35,36]. More efficient production and sales processes can be achieved through the reintegration of scattered local land resources, and by combining different sales models, existing self-production and self-sales business models can be expanded to achieve a more scalable, organized, and professional sales model. However, it should be noted that the effectiveness of sales model innovation is constrained by two factors: (1) ecological red lines limit the physical space for land integration; (2) the special regulations of national parks increase the institutional costs of market access, which could lead the current industry into the "smiling curve" trap, where farmers are locked into production stages with the lowest added value.

Agricultural support policies can safeguard agricultural production, which is characterized by cyclicality and vulnerability [37]. Within the scope of the Northeast China Tiger and Leopard National Park, agricultural safeguard policies have a high degree of coverage, but such universal policies have difficulty meeting diversified needs for sustainable local development. The root cause lies in the institutional friction between the special governance structure of national parks and traditional agricultural support policies. National Park governance prioritizes "environmental protection" while traditional agricultural policies focus on "food security" and "increasing farmers' income". We recommend establishing a "special ecological zone" policy framework to help farmers further share production risks and encourage the development of the local specialty agricultural economy by improving the existing agricultural support policy system.

The development of industrial clusters can stimulate the production enthusiasm and livelihood sustainability of local farmers [38]. However, in practical terms, planning and implementation for increasing the added value of agricultural products and developing a full industrial chain model suitable for local characteristic industries need to be tailored to local conditions. For characteristic agricultural products in the Hunchun area, given the particularity of the location, several factors limit industrial development, making it relatively difficult to advance. Meanwhile, in terms of ecotourism, given the uniqueness of locally protected species, it is difficult for tourists to see them at close range, making it challenging to realize the value of ecotourism. These findings provide new entry points for subsequent research. We recommend further exploring the adaptive development path of characteristic industries in protected areas from an institutional perspective.

7. Recommendations

This subsection outlines actionable strategies to address the challenges identified in the discussion. The recommendations are organized into three key areas: optimizing participation mechanisms, innovating industrial upgrading pathways, and establishing long-term participation frameworks. These proposals aim to improve the effectiveness of policies and promote the sustainable development of national park communities. It should be noted that these suggestions require further research to receive more support. Meanwhile, considering that the Northeast Tiger and Leopard National Park is located on the border between China and Russia; in order to promote the overall and integrity protection of the ecosystem, it is necessary to consider the connection between the policies of the two countries. Russia emphasized the cross-border protection of Northeast tigers in the "Tiger Conservation Strategy of the Russian Federation", and the leaders of China and Russia also proposed to strengthen cooperation in species cross-border protection during

their meeting in 2019. Therefore, when considering policy formulation, it is necessary to take into account the connection and cooperation with Russia's relevant policies and further enrich the integrity of China's policies.

7.1. Optimizing the Design of the Participation Mechanism

To increase farmers' enthusiasm for participation, it is important to strengthen the driving role of cooperatives and leading enterprises. Specific recommendations include the following. Establish a special support fund to help cooperatives provide technical training and market access services for farmers while promoting the "cooperative + farmer" model to achieve shared benefits through land shares and contract farming. For leading enterprises, mandatory long-term cooperation agreements with local farmers should be established to clarify benefit distribution and prevent the marginalization of farmers' interests. Differentiated policies are essential, i.e., subsidies and low-interest loans should target low-income and elderly farmers for prioritized project participation while entrepreneurship incubation (e-commerce training, ecotourism permits) should target educated farmers to cultivate community leaders.

7.2. Innovating the Pathways of Industrial Upgrading

On the sales front, contract farming and equity-based cooperative farms should be promoted. In addition, regional agricultural trading platforms should be established to reduce intermediaries, and pilot "reverse land leasing + equity cooperation" models where village collectives consolidate land to attract social capital. For industrial upgrading, nonintrusive tourism (birdwatching, nature education) with strict visitor restrictions should be developed to protect tiger habitats while training farmers as eco-guides. We can also conduct economic evaluations of industrial transformation based on existing experience and under the premise of a closed-loop model, to increase the reliability of future industrial transformation choices. Furthermore, cattle farming should be leveraged to create organic beef brands and immersive ranch experiences, along with offering tax incentives for deep-processing enterprises that prioritize local hiring. In the future, we will further increase promotional activities on green product labeling to enhance public acceptance of eco-friendly products.

7.3. Establishing Long-Term Participation Mechanisms

A coordination committee (farmers, government, reserve management) should be established for regular policy reviews and benefit sharing, in addition to implementing "community co-management" granting oversight of conservation activities. Technologically, a smart agriculture platform with blockchain traceability should be developed for "tiger-friendly" certification, and cross-border ecotourism with Russian reserves should be promoted alongside establishing "economic enclaves" to relocate intensive industries, thus alleviating ecological pressures. In terms of the ecological protection participation mechanism, after the establishment of Northeast Tiger and Leopard National Park, strict restrictions were imposed on yellow cattle farming in the mountains, effectively promoting the growth of local grassland vegetation. However, this will to some extent increase the risk of grassland fires. Therefore, in the future management process, it is necessary to prevent and regulate the grassland ecological environment in advance, and limited grazing can be carried out appropriately to reduce fire hazards.

To ensure sustainable engagement, a coordination committee comprising farmers, government representatives, and reserve management should be established. This committee would oversee regular policy reviews and facilitate equitable benefit-sharing mechanisms. Additionally, adopting a "community co-management" model would empower local stakeholders to actively participate in conservation activities. On the technological front, devel-

oping a smart agriculture platform integrated with blockchain traceability can enhance the credibility of "tiger-friendly" certifications. Furthermore, fostering cross-border ecotourism collaborations with Russian reserves and creating "economic enclaves" to relocate intensive industries can significantly reduce ecological pressures.

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Fields of Conflict: Public Attitudes and Economic Impacts of Human–Wildlife Conflict on Rural Livelihood in District Lakki Marwat, Pakistan

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Abstract: Human–wildlife conflict poses significant ecological and socio-economic challenges, particularly in rural communities where agriculture and livestock rearing form the backbone of livelihoods. Despite the growing importance of this issue, District Lakki Marwat remains an unexplored area of northwest Pakistan. This study aims to fill this gap by systematically assessing the status, economic impacts, and community perceptions of five wildlife species: wild boar (*Sus scrofa*), grey wolf (*Canis lupus*), golden jackal (*Canis aureus*), striped hyena (*Hyaena hyaena*), and red fox (*Vulpes vulpes*). Using semi-structured surveys with 117 respondents, we analyzed species prevalence, perceived danger levels, crop damage patterns, and predation impacts on livestock and poultry. The findings revealed that wild boars were identified as the primary contributors to agricultural damage, with total annual crop losses surpassing the economic impacts attributed to the studied carnivores. On average, each surveyed household experienced an annual loss of PKR 4510.38. For the 39% of households reporting crop damage, the annual loss per reported household was PKR 11,727, which was higher than the average annual loss across all households, underscoring the severity of the impact on those specifically affected by the wild boar-related crop damage. Notably, community attitudes were most negative toward wild boars, a pattern driven by the economic burden of crop losses, challenging the conventional focus on carnivores as the primary conflict species. A Pearson's X^2 test confirmed strong associations between species and perceived danger levels, while regression analysis demonstrated an association between crop damage and negative attitudes. Traditional deterrents like thorn fences were found ineffective against wild boars. More advanced methods, including game-proof fencing, trenches, bio-fencing, crop rotation, audio and visual deterrents, taste and order repellents, and watchtowers combined with group vigilance, are recommended to reduce crop damage. Integrating these approaches with community-based education, habitat management, and government-supported compensation schemes can mitigate wild boar impacts. This study contributes new insights into multi-species HWC dynamics, demonstrating that community perceptions are primarily shaped by the economic impact of a species, regardless of whether it is a carnivore or an omnivore. The attitudes of local communities are driven by the financial losses incurred, rather than the species' behavior or ecological role. This study underscores the need for collaborative efforts to reduce human–wildlife conflict, foster coexistence, and ensure ecological balance in vulnerable rural areas.

Keywords: wildlife; conflict; economic losses; human perceptions; conservation; rural communities; Lakki Marwat; Pakistan

1. Introduction

Wildlife species hold significant ecological, economic, scientific, and cultural value and play a pivotal role in maintaining ecosystem balance [1] by regulating prey populations and supporting biodiversity [2–4]. However, without effective management, they can cause substantial economic losses, resulting in human–wildlife conflict (HWC) [5]. HWC is more prevalent in rural areas, where a large portion of the population depends on livestock rearing and agricultural activities for their livelihood [6]. Conflicts between agrarian interests and wildlife conservation are intensifying worldwide, due to significant economic losses from crops, livestock, and property damage [7–11]. The stakes are higher in developing countries, where rural communities are highly reliant on agricultural crops and livestock rearing for their livelihood [12]. Consequently, these losses breed negative attitudes and perceptions among the agro-pastoral populations. Human–wildlife conflict has significant socio-economic consequences, especially in rural communities where agriculture and livestock are the primary livelihood sources. Understanding human attitudes toward wildlife, including economic impacts and cultural values, is critical for developing effective management strategies [13].

In addition to wildlife behavior, human activities significantly exacerbate HWC. The expansion of agricultural land, infrastructure development, and overgrazing by livestock are key drivers of conflict, as they directly encroach upon natural wildlife habitats, reducing the available space and resources for wildlife. Illegal hunting of natural prey species further strains wildlife populations, particularly large carnivores, which are often forced to prey on livestock when their natural food sources diminish. Additionally, livestock management practices such as bringing animals into wildlife habitats for grazing increase their vulnerability to predation, thereby escalating the conflict. These human-driven factors are critical to understanding the dynamics of HWC, as they create situations where both wildlife and humans bear the costs of conflict. HWC is a global conservation challenge, especially in areas where wildlife coexist with humans [14–16]. Large mammalian carnivores including grey wolves (*Canis lupus*), lions (*Panthera leo*), jaguars (*Panthera onca*), snow leopards (*Panthera uncia*), and common leopards (*Panther pardus*) are known as the primary suspects for livestock depredation [17–20], whereas wild boars are known as a serious threat to crops [9,10,21–23]. Economic losses due to predators through livestock predation and crop damage by wild boars vary widely in nature and intensity across the globe. However, these losses are very severe when they occur in rural areas, where people heavily rely on livestock rearing and agricultural products for their livelihoods [24].

For communities vulnerable to human–wildlife conflicts, wildlife-induced damage can be financially devastating, jeopardizing their survival, wildlife coexistence, and conservation efforts [17,25–27]. In some regions, livestock predations cause economic losses of up to 18% of annual household income, straining pastoral communities already living below the poverty line, while wildlife frequently exacerbate hardships by damaging crops [27]. Retaliatory killings remain a leading threat to predator populations, directly undermining global conservation efforts and contributing to population decline or even extinction of numerous wildlife species [28–30]. These challenges highlight the urgency of well-designed and well-thought-out conservation efforts, particularly in areas where livelihoods and biodiversity are deeply intertwined. In regions such as South Asia, similar conflicts are escalating due to growing populations and expanding agricultural frontiers,

which increasingly encroach upon wildlife habitats [7,11,31]. Studies from India [7,8,32,33] and Nepal highlight comparable challenges, where wildlife species are perceived as significant threats to crops and livestock, driving retaliatory actions and deepening negative perceptions of wildlife among local communities

Human–wildlife conflict is particularly severe in Pakistan due to rapid population growth, and the conversion of natural habitat into agricultural land and infrastructure. These changes increase the frequency of human–wildlife encounters, most of which have adverse effects on both humans and wildlife. In Pakistan, where agriculture contributes 22.04% to the gross domestic product (GDP) and supports 35.9% of employment, the stakes of HWC are particularly high [34,35]. Approximately 62% of the country's population resides in rural areas and depends directly or indirectly on agro-pastoral livelihoods. Pakistan's rich biodiversity includes several wildlife species that frequently damage crops and livestock, leading to substantial retaliatory killings [5,31]. Among the wildlife species contributing to HWC, wild boars (*Sus scrofa*) are particularly destructive, causing significant crop losses across their rapidly expanding range [36], while carnivores such as the grey wolf (*Canis lupus*), golden jackal (*Canis aureus*), striped hyena (*Hyaena hyaena*), and red fox (*Vulpes vulpes*) prey on livestock, pets, and poultry, further exacerbating economic and ecological tensions in agro-pastoral regions [37,38].

This study focused on District Lakki Marwat, where five species—grey wolf, golden jackal, striped hyena, red fox, and wild boar—have been identified as significant contributors to economic losses to the rural communities. Despite ongoing wildlife-related economic losses, Lakki Marwat has remained largely unstudied in terms of human–wildlife conflicts. This study attempts to fill this gap by providing a systematic assessment of WHC in the study area. Moreover, while many HWC studies primarily focus on a single species or only large carnivores, this research adopts a broader approach by incorporating both carnivores and an omnivorous species—wild boars—to provide a more comprehensive understanding of conflict dynamics in agro-pastoral landscapes. By surveying local communities, we aimed to quantify the impacts of these species, evaluate the economic consequences of livestock predation and crop damage, and assess community attitudes toward wildlife. The findings of this study provide critical insights into species-specific conflict dynamics and offer a foundation for targeted, evidence-based mitigation strategies that balance the needs of biodiversity conservation and community livelihoods. Our research adds to the growing body of knowledge on HWC [8,33,37–39] and emphasizes the global relevance of the issue, with lessons that can be applied to other regions facing similar challenges in balancing conservation and rural livelihoods.

2. Materials and Methods

2.1. Study Area

This study was carried out across the rural communities of District Lakki Marwat in the southern regions of Khyber Pakhtunkhwa (Figure 1). This district has an area of 3164 km^2 and a total of 131,800 households. It has a population of 1,040,856, resulting in a population density of approximately 329 individuals per square kilometer. The district's predominantly rural population relies on agriculture and livestock, producing crops like wheat, maize, peanuts, and chickpeas, along with cash crops such as melons and vegetables, with potential for growth through improved irrigation [40].

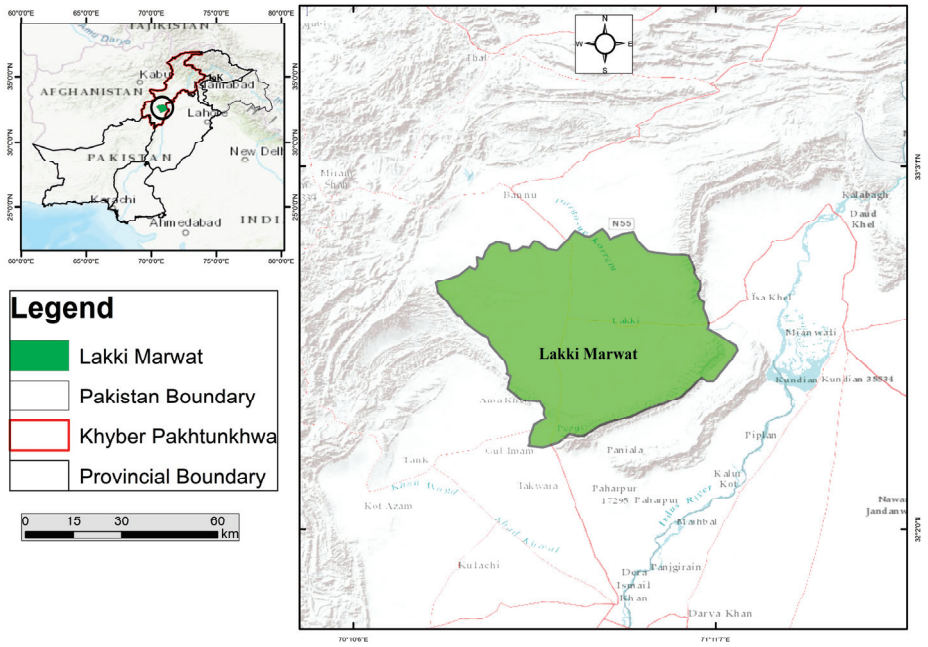

Figure 1. Map of the study area.

2.2. Field Surveys

We interviewed a total of 117 respondents from the rural communities of District Lakki Marwat. It is crucial to emphasize that the survey was deliberately designed to focus on rural villages with distinct agricultural and ecological characteristics, which are integral to the research objectives. These selected villages are representative of the areas most impacted by human–wildlife conflict, primarily due to their higher levels of agricultural and livestock activity. Additionally, the ecological richness of these regions, characterized by diverse habitats and intensive land use, makes them particularly relevant for understanding the complex interactions between human activities and wildlife. By concentrating on these specific villages, this study aimed to obtain a more targeted and in-depth analysis of the local dynamics driving human–wildlife conflict, which would provide more nuanced insights compared to a broader, less focused sampling approach. The inclusion of 5–10% of households from each surveyed village ensures that the sample is both statistically meaningful and representative, offering a robust basis for assessing the key factors contributing to human–wildlife conflict within these high-impact areas [37,38]. This approach allows for a deeper understanding of the localized phenomena, ensuring the findings are relevant and applicable to the regions under study. Due to social constraints and cultural context, only male respondents were interviewed, as they are primarily involved in agricultural and related activities [37,38].

Questionnaire surveys are useful in collecting information about the presence, tolerance, and perception of local communities toward predators [38,41]. Moreover, the local people could be a valuable source of information regarding their ecosystems [42,43]. Participants were selected based on their pre-existing knowledge about wildlife species reported from the study area including grey wolf, golden jackal, red fox, striped hyena, and wild boar [44]. The respondents included herders, farmers, businessmen, government servants, and local hunters. The interviews were conducted using a predesigned, semi-structured questionnaire form having a series of open-ended questions. To obtain credible information on the species in question, color photographs of wild boars along with other species including grey wolf, golden jackal, common leopard, striped hyaena, and red fox were shown to respondents, who were then asked to identify them [38]. Before questioning, respondents were informed about this study's purpose, the anonymity of the

data, and their freedom to withdraw from the survey at any point, which helps prevent biased responses and exaggerated information [42]. Formal consent from each respondent was obtained prior to commencing the questionnaire (Supplementary Materials, Table S1).

The questionnaire contained a total of 15 items divided into several sections (Supplementary Materials, Table S2). The initial section gathered demographic data of the respondents, such as age, household size, education level, profession, monthly income, number of earning members in the family, and agriculture land ownership. The next main section of the questionnaire inquired about the number of sightings of the species and their status (absent, rare, and common). Then, they were asked about the perceived danger of the species to their livestock and crops, and the extent of damage and associated estimated economic losses due to particular species in the last two years. Economic losses due to wildlife-induced damage were estimated based on the market prices of affected crops and livestock. The respondents were requested to provide the estimated quantity of crop damage due to wildlife and associated estimated economic loss. For accuracy, we cross-checked the reported crop prices with those in the respective Union Council (lowest administrative unit in local governments) markets, where prices are generally uniform due to government regulation and price control. For livestock, as prices are typically determined through negotiation between buyers and sellers, we relied on the estimated prices provided by the respondents. Additionally, the first and fourth authors are residents of the surveyed area, providing them with firsthand knowledge of the typical price ranges for both crops and livestock. Moreover, the respondents were asked about the desired outcome for species population trends (want to increase, decrease, maintain, or eliminate). The intensity of each species' threat to crops and livestock was measured on a five-point Likert scale [45], with categories ranging from "no threat" to "extreme threat". This scale also assessed the dependency of respondents on agriculture and livestock for their livelihood and allowed for comparisons in the severity of perceived damage due to the species. The interviews were taken from the respondents in the study area with the help of written semi-structured questionnaires designed with open-ended questions [37,38,42,46].

2.3. Data Analysis

The data were analyzed in R (4.3.2) using packages like *dplyr*, *ggplot2*, *vcd*, and *gridExtra* [47] for data management, analysis, and visualizations. For statistical insights, a Chi-squared test was used to assess the relationship between the species status reported by the respondents and their attitude toward its population trend. We conducted multiple linear regression analysis using R to assess the relationship between economic losses and negative attitudes toward wildlife. The dependent variable (Y) was negative perceptions toward wildlife, while independent variables (X) included economic losses due to crop damage (PKR), economic losses due to livestock predation (PKR), land size (hectares), livestock ownership (number of livestock), and household income (PKR) (Equation (1)). For analysis, the ordinal categories for negative attitudes were coded as numerical values (eliminate = 4, reduce = 3, maintain = 2, and increase = 1), allowing them to be treated as a continuous variable in the regression model. We used functions from the *ggplot2* and *ggpubr* packages in R to visualize relationships between variables. Scatter plots with linear regression lines and confidence intervals were generated to illustrate these relationships, and Pearson correlation coefficients [48] and *p*-values were calculated to quantify the strength and significance of associations. The geographical map of the studied area was developed using the Arc Global Positioning System (Arc GIS) (Version 10.5). Equation (1) was calculated as follows:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \varepsilon \quad (1)$$

where Y (dependent variable): negative attitudes toward species (measured on a Likert scale); X_1 (independent variable): agricultural land size (hectares); X_2 (independent variable): livestock herd size (total number of livestock owned); X_3 (independent variable): total economic losses (crop + livestock PKR); X_4 (independent variable): species type (categorical variable: wild boar, grey wolf, etc., converted into dummy variables); β_0 (intercept): baseline level of negative attitudes when all predictors are zero; β_1 to β_4 (regression coefficients): estimated effect of each independent variable on negative attitudes; and ε (error term): residual variance not explained by the model.

3. Results

3.1. Demographic Details of the Surveyed Respondents

A total of 117 respondents volunteered for the surveys (Table 1). The respondent profession data indicate that the majority of participants identified as farmers, accounting for 38.46% (45 respondents). Herders formed the second-largest group at 24.79% (29 respondents), followed by businessmen at 19.66% (23 respondents) and government servants at 17.09% (20 respondents). The analysis of agricultural land ownership among respondents revealed that the largest proportion of participants (45.30%) own land in the 1 to 8.1-hectare range (1 to 20 Kanal), totaling 53 respondents. This is followed by an 8.1 to 12.1-hectare range (21 to 30 Kanal), representing 27.35% (32 respondents). Respondents owning land 12.1 hectares (31 Kanal and above) account for 23.08% (27 respondents), while a small proportion (4.27%, five respondents) reported having no agricultural land. An analysis of livestock ownership among respondents shows that sheep are the most commonly owned livestock, accounting for 42.02% of the total (321 animals). This is closely followed by goats, which represent 38.74% (296 animals). Cows and donkeys are less prevalent, contributing 12.43% (95 animals) and 6.81% (52 animals) to the total livestock count, respectively.

Table 1. Demographic details of surveyed respondents, including profession, land ownership, and livestock holdings. The table highlights the distribution of respondents by occupation, size of agricultural land owned, and the number of livestock types, reflecting the agro-pastoral nature of the surveyed population.

Profession	**No. of Respondents**	**Proportion (%)**
Farmer	45	38.46
Herder	29	24.79
Businessman	23	19.66
Govt servant	20	17.09
Total respondents	117	
Land Size (Hectares)	--	--
Zero	5	4.27
1 to 8.1 (1 to 20 Kanal)	53	45.3
8.1 to 12.1 (21 to 40 Kanal)	32	27.35
12.1 and above (41 Kanal and above)	27	23.08
Total respondents	117	--
Livestock	Number of Livestock	Proportion (%)
Goat	296	38.74
Sheep	321	42.02
Cow	95	12.43
Donkey	52	6.81
Total	764	--

3.2. Species Status as Perceived by Respondents

The analysis evaluated community perceptions of species' statuses (common, rare, and absent) across five species: wild boar, striped hyena, grey wolf, golden jackal, and red fox (Figure 2). Descriptive statistics revealed significant variation in the frequency of responses across categories. Wild boars and golden jackals were most frequently reported as "common," with 93 and 103 responses, respectively. In contrast, grey wolves and striped hyenas received higher "absent" responses (43 and 57, respectively), reflecting a general perception of lower prevalence in the study area. The "rare" status showed moderate frequency for most species, with grey wolves receiving the highest (51 responses).

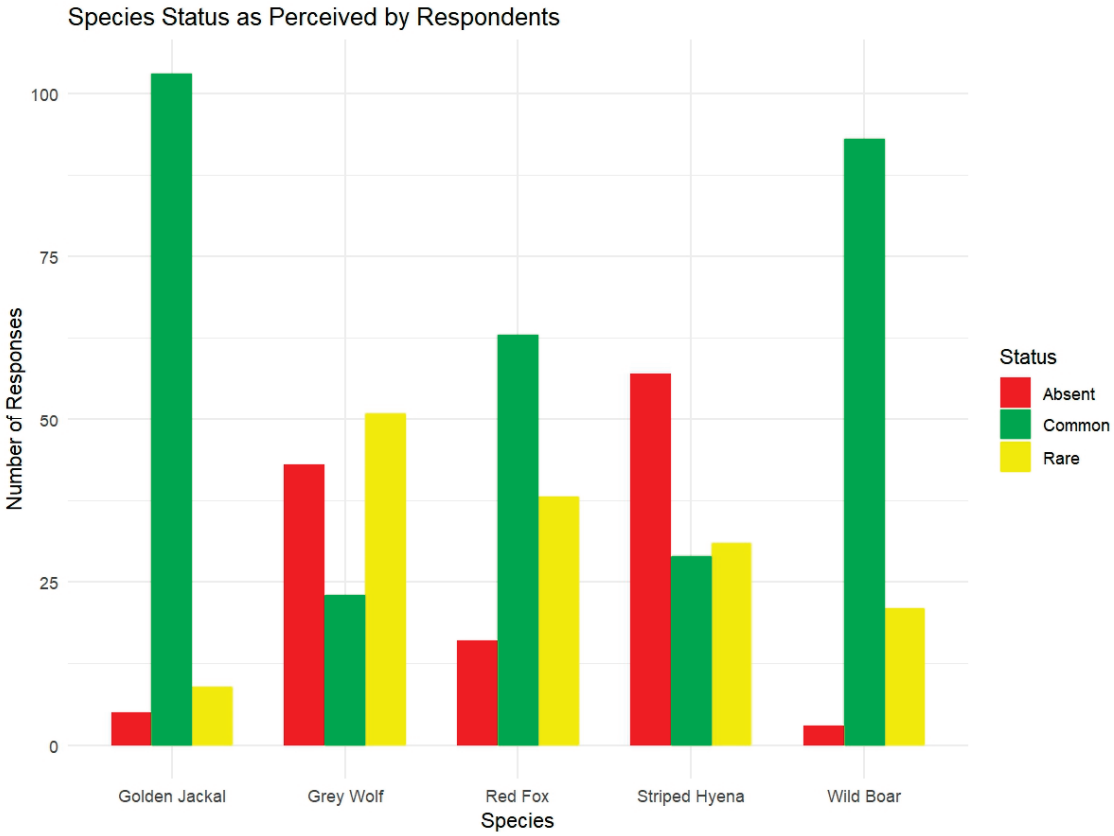

Figure 2. Species status as perceived by respondents. Distribution of responses for each species' status across the surveyed respondents. The bars representing "common", "rare", and "absent" are distinguished by varying grayscale intensities.

3.3. Perceived Danger of Species to Livestock and Crops

Community perceptions of species' danger to livestock were analyzed across five species. The distribution of responses highlights significant differences in perceptions about the species in the study area. Grey wolves (78 responses) and golden jackals (67 responses) were most frequently categorized as posing extreme danger, while wild boars were predominantly perceived as posing a negligible danger to livestock, with 109 responses (Figure 3, Supplementary Materials, Table S3). Striped hyenas received mixed perceptions, with the majority of respondents categorizing them as posing low danger (89 responses). A Pearson's Chi-squared test was conducted to evaluate the association between species and their perceived danger rankings. The results indicate a highly significant association ($\chi^2 = 901.29$, df = 20, $p < 2.2 \times 10^{-16}$), suggesting that perceptions of danger varied significantly across species. The analysis of crop damage perceptions (perceived threat/danger of a species for crop damage) revealed that only wild boars were held responsible, with the majority of responses categorizing them under extreme danger

(103 responses) and high danger (14 responses). Other species, such as striped hyena, grey wolf, golden jackal, and red fox, were not perceived as contributors to crop damage.

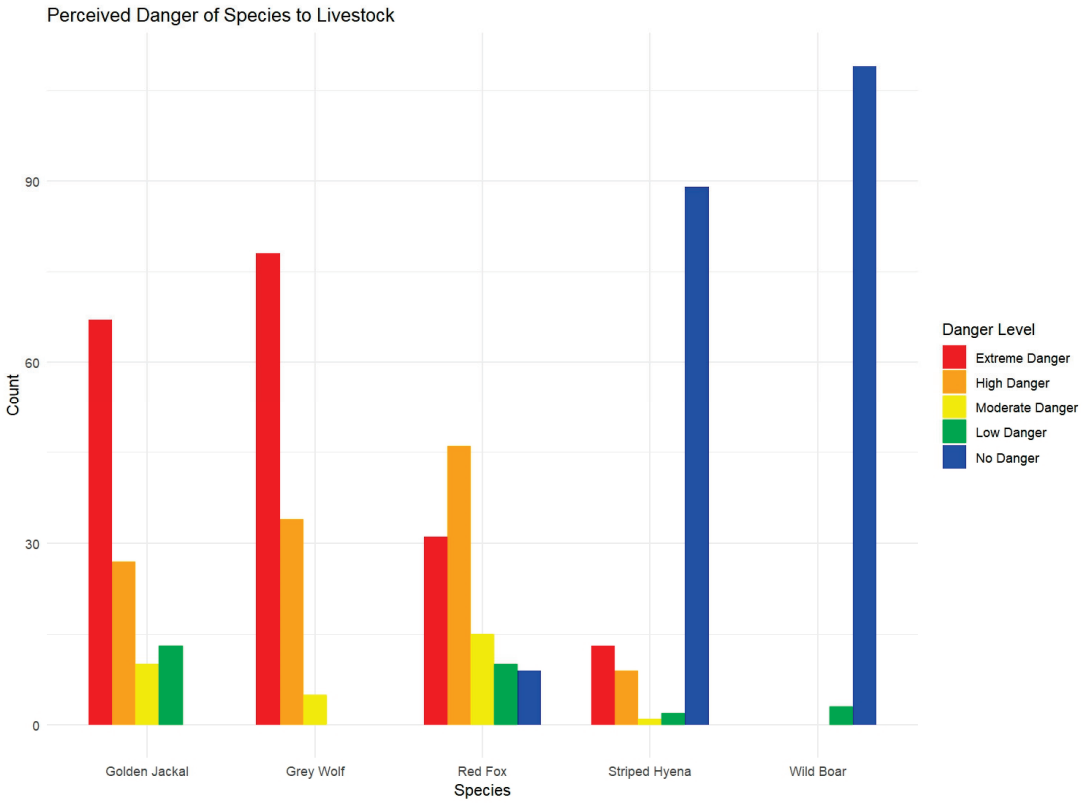

Figure 3. Perceived danger levels of wildlife species to livestock were categorized into five levels: extreme danger, high danger, moderate danger, low danger, and no danger. The graph illustrates the frequency of responses for each species, highlighting the grey wolf and golden jackal as perceived to pose extreme danger.

3.4. Temporal and Seasonal Patterns in Crop Raiding and Damage

The analysis of crop raiding events revealed a clear nocturnal tendency, with night accounting for 48.72% (57 events) of all incidents, followed by morning (22.22%, 26 events), evening (17.95%, 21 events), and day being the least frequent (11.11%, 13 events) (Supplementary Materials, Table S4). A Chi-Square Goodness-of-Fit test confirmed these differences as statistically significant ($\chi^2 = 38.043$, df = 3, $p < 0.001$), indicating an uneven distribution of raiding events across times of the day. The seasonal crop damage analysis identified spring as the most affected season (Supplementary Materials, Table S4), accounting for 35.04% (41 incidents), followed by autumn (31.62%, 37 incidents), winter (17.95%, 21 incidents), and summer with the lowest damage (15.38%, 18 incidents). A Chi-Square Goodness-of-Fit test ($\chi^2 = 13.427$, df = 3, $p = 0.0038$) highlighted significant seasonal variations, emphasizing spring and autumn as critical periods for crop damage mitigation.

3.5. Predation Patterns and Economic Impact of Species

The analysis of predation patterns revealed notable distinctions among the studied predators regarding their impact on livestock, pets, poultry, and crops (Table 2). Grey wolves caused an estimated PKR 113,000 in losses over two years, affecting 5% of the surveyed households. The annual loss per household due to grey wolves was PKR 56,500 (or USD 281.1), with affected families incurring a financial burden of PKR 9417 annually on average. Golden jackals and red foxes primarily target poultry, with predation losses of PKR 37,100 (approximately USD 92.3) for golden jackals and PKR 25,900 (around USD

92.5 for red foxes. Golden jackals affected 20% of the surveyed households, while red foxes were reported by 16% of the households. The average annual loss per affected household was PKR 807 for golden jackals and PKR 682 for red foxes. Striped hyenas caused an estimated loss of PKR 55,000 (approximately USD 136.8) over the two years. Striped hyenas impacted 4% of the surveyed households, resulting in an average annual loss of PKR 5500 per affected household.

Table 2. Economic losses caused by different wildlife species, categorized by livestock predation, pet losses, poultry predation, and crop damage (in PKR) as reported by respondents over the past two years.

Economic Impact	Species Grey Wolf	Golden Jackal	Striped Hyena	Red Fox	Wild Boar
Livestock (PKR)	113,000	-	-	-	-
Pets (PKR)	-	-	55,000	-	-
Poultry (PKR)	-	37,100	-	25,900	-
Crop damage (PKR)	-	-	-	-	1,055,429
Total loss (PKR)	113,000	37,100	55,000	25,900	1,055,429
Annual loss * (PKR)	56,500	18,550	27,500	12,950.00	527,714.50
Annual loss * (USD)	281.09	92.29	136.82	64.43	2625.45
Loss per surveyed HH/year (PKR)	482.91	158.55	235.04	110.68	4510.38
Households reporting the loss ** (percent)	5%	20%	4%	16%	39%
Annual loss per reported household *** (PKR)	9417	807	5500	682	11,727

*: Annual loss (PKR/USD) represents the average economic loss per household across all 117 surveyed respondents, regardless of whether they reported experiencing losses. **: Households reporting the loss represents those households that reported losses due to wildlife. ***: Annual loss per reported household reflects the average actual annual loss per household among those who specifically reported wildlife-related damages.

In contrast, wild boars are solely responsible for significant crop losses, which exceed all other forms of wildlife damage combined. The estimated total crop damage caused by wild boars amounts to PKR 1,055,429 (equivalent to USD 5250.89) over the two years (Figure 4, Supplementary Materials, Table S5). Wild boars have caused substantial losses to crops, especially maize and groundnuts, with the highest financial impact from maize losses, amounting to PKR 265,973 (approximately USD 1323.25). The total annual loss due to crop damage caused by wild boars was PKR 527,714.5 (USD 2625.45). On average, each of the 117 surveyed households experienced an annual loss of PKR 4510.38. A significant 39% of the households surveyed reported crop losses due to wild boars. The annual loss per reported household was PKR 11,727, which was notably higher than the average annual loss across all surveyed households, underscoring the severity of impact on those specifically affected by wild boar-related crop damage.

3.6. Community Attitudes Toward Species Population

This study examined community attitudes regarding five species and revealed that the highest count for "eliminate (eliminate the entire population of the species from the area)" was recorded for wild boar (78 responses), while "maintain" attitudes were most frequent for golden jackal (42 responses) (Figure 5, Supplementary Materials, Table S6). Attitudes toward population "increase" remained low across all species, with the highest being for golden jackal (25 responses).

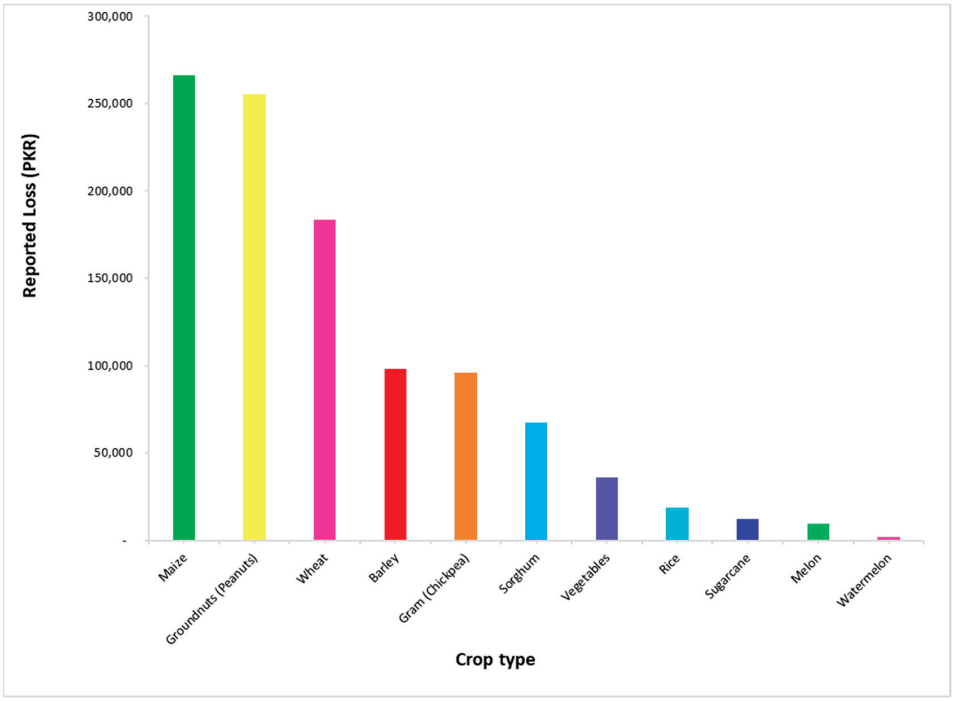

Figure 4. Reported financial losses across various crop types caused by wild boars (in PKR).

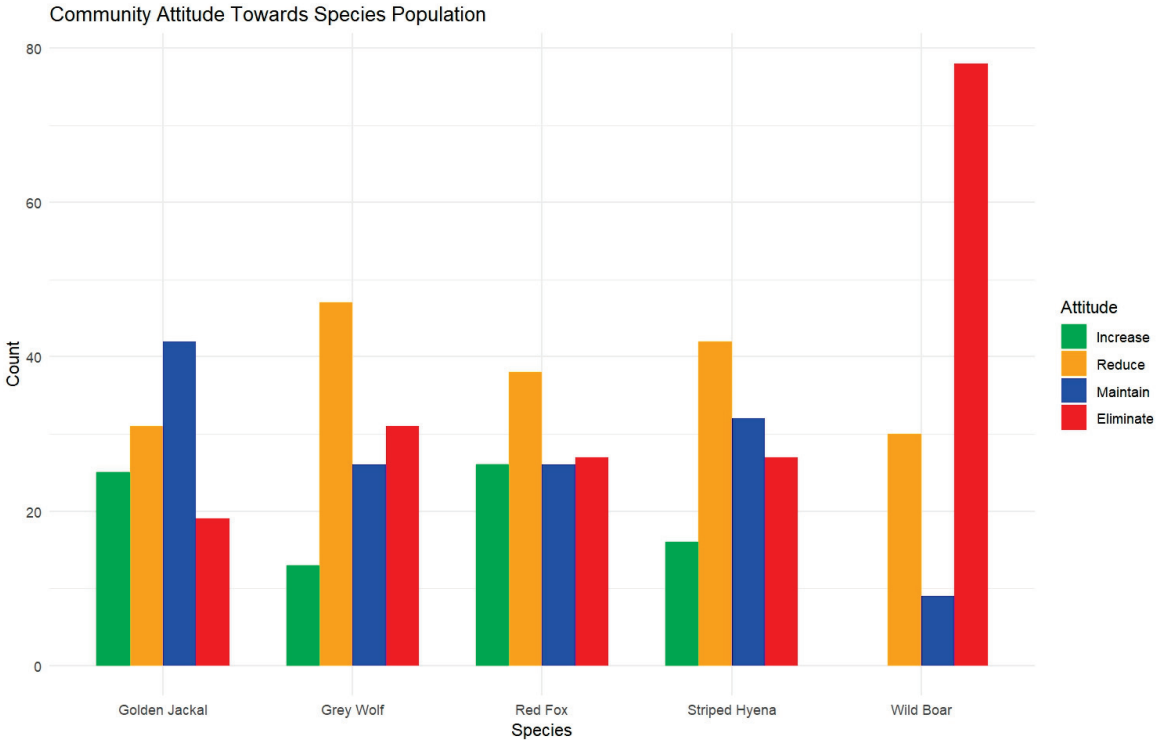

Figure 5. Community attitude toward species population. The varying grayscale tones for the four attitudes illustrate the response distribution across species and attitudes.

A Chi-squared test revealed a highly significant association between wildlife species and community attitudes ($\chi^2 = 215.68$, df = 32, $p < 2.2 \times 10^{-16}$), highlighting that negative perceptions vary substantially across species. An ANOVA test confirmed significant differences in negative attitudes across species (F = 637.4, $p < 0.001$). Pairwise t-tests with Bonferroni adjustments indicated statistically significant differences between negative attitudes toward wild boars and all other species ($p < 0.001$), further underscoring the dis-

proportionately negative perception toward wild boars. The analysis of negative attitudes toward wildlife species revealed that wild boars experienced the highest negative perception, with an aggregated score exceeding 200, significantly differing from all other species ($p < 0.001$) (Figure 6). The negative attitudes score for each species is derived from the sum of individual ratings (1–4) provided by the respondents, where higher values indicate more negative attitudes. Grey wolves and striped hyenas also received relatively high negative scores, reflecting moderate concerns about their impact on livestock and human–wildlife conflict. In contrast, red foxes and golden jackals were perceived less negatively, with scores below 130, suggesting they are considered less threatening. The negative attitude score represents the sum of respondents' ratings based on perceived threat and the extent of damage caused by each species. The multiple linear regression model revealed significant predictors of negative attitudes toward wildlife species, explaining 79% (Adjusted $R^2 = 0.79$) of the variance (Table 3). Total economic losses (crop damage and livestock predation combined) emerged as the strongest predictor of negative attitudes ($\beta = 0.48$, $t = 6.86$, $p < 0.001$), indicating that financial burdens significantly influence community perceptions of wildlife. Among the socio-economic variables, livestock herd size was positively associated with negative attitudes ($\beta = 0.25$, $t = 4.17$, $p < 0.001$), suggesting that larger herds correlate with higher negative perceptions. Conversely, agricultural land size showed a significant negative relationship ($\beta = -0.10$, $t = -2.50$, $p = 0.013$), indicating that households with larger landholdings tend to exhibit greater tolerance toward wildlife. When considering species type, wild boars were associated with the highest negative attitudes ($\beta = 0.75$, $p < 0.001$), reflecting their significant impact on crop damage and subsequent economic losses. Among carnivores, grey wolves ($\beta = 0.32$, $p = 0.002$) and striped hyenas ($\beta = 0.28$, $p = 0.003$) were the most negatively perceived, likely due to their predation on livestock and domestic animals. In contrast, red foxes and golden jackals were associated with lower negative perceptions, and their coefficients were not statistically significant ($p > 0.05$). These findings highlight the critical role of economic losses and species type in shaping community attitudes toward wildlife, emphasizing the need for targeted, species-specific mitigation strategies to address human–wildlife conflict effectively.

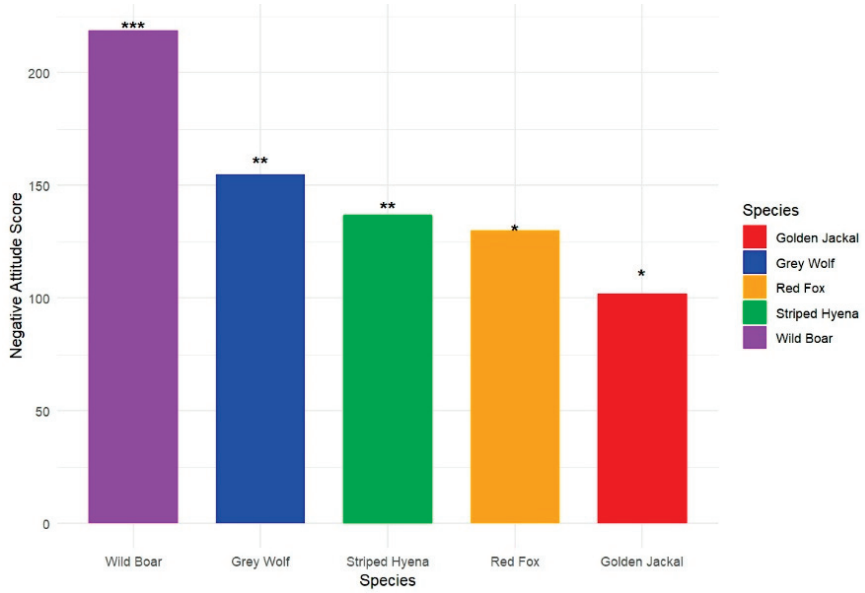

Figure 6. Negative attitudes (sum of reduced and eliminated scores) toward species, based on the sum of individual ratings (ranging from 1 to 4 per respondent). The total negative score for each species reflects the aggregate of respondent attitude, with the higher scores indicating more negative views. Statistical significance is marked above the bars with asterisks. *** ($p < 0.001$): very highly significant; ** ($p < 0.01$): highly significant; and * ($p < 0.05$): significant.

Table 3. The results of multiple linear regression analysis predicting negative attitudes toward wildlife species. The dependent variable is the negative attitude score. Predictor variables include total economic losses (PKR), agricultural land size (hectares), livestock herd size, and species type. Species type was modeled using dummy variables, with wild boar as the baseline. The model explains 80% of the variance in negative attitudes ($R^2 = 0.80$). Statistically significant predictors are marked with p-values < 0.05.

Predictor Variable	Coefficient (β)	Standard Error	t-Value	*p*-Value
Total economic losses (PKR)	0.48	0.07	6.86	<0.001
Agricultural land size (hectares)	−0.1	0.04	−2.5	0.013
Livestock herd size	0.25	0.06	4.17	<0.001
Species type (dummy variables)	Wild boar: 0.75	0.11	6.82	<0.001
	Grey wolf: 0.32	0.1	3.2	0.002
	Striped hyena: 0.28	0.09	3.11	0.003
	Red fox: 0.15	0.08	1.88	0.061
	Golden jackal: 0.10	0.07	1.43	0.155
Intercept	1.9	0.2	9.5	<0.001
$R^2 = 0.80$, Adjusted $R^2 = 0.79$, $F = 56.73$, $p < 0.001$				

4. Discussion

This study identified, quantified, and analyzed the magnitude of human–wildlife conflict in rural communities of District Lakki Marwat located in northwest Pakistan. It focused on the economic impacts, crop damage, predation patterns and intensities, and communities' perceptions and attitudes toward the species of grey wolf, golden jackal, striped hyena, red fox, and wild boar. This study employed the questionnaire survey method, which is a widely utilized approach in studies addressing similar objectives [37,38]. Community-based surveys allow locals to express their perspectives about wildlife, which are critical for designing effective management plans [49–51]. This study offers a unique perspective by focusing on four carnivore species and one omnivore. By integrating both carnivores and omnivores, this work provides a broader understanding of multi-species HWC dynamics and highlights how different species contribute to economic losses and local perceptions. This study highlights that community perceptions toward wildlife are driven by the economic impacts of the species, whether carnivore or omnivore, rather than behavior or ecological role.

Communities' attitudes toward wildlife play a pivotal role in determining the success or failure of conservation efforts. Negative perceptions, particularly fueled by economic losses, often result in retaliatory killings and reduced local support for conservation [3,39]. For instance, retaliatory killings of grey wolves have resulted in population declines across their distribution range [52,53]. Moreover, in some parts of Europe, negative public attitudes toward grey wolves have caused conflicts over reintroduction programs [54,55]. HWC causes significant economic losses, with damages to livestock and crops from wildlife species [46] ranging from 3% to 18% of income for rural communities [27], leading to negative perceptions and attitudes toward wildlife [56]. These losses are primarily due to the direct impact of wildlife, while human responses such as preventative measures also contribute to the economic burden.

In our study, wild boars and golden jackals were most frequently reported as common, while grey wolves and striped hyenas were perceived as rare or absent. This variation in the status of the studied species could be attributed to habitat availability, prey density, and human activity in the region. Wild boars' adaptability to human-dominated landscapes, coupled with their high reproductive rates and lack of natural predators, likely explains their abundance [57]. Golden jackals are also reported from the area [58].

Grey wolves and golden jackals were identified as extreme danger to livestock. These findings align with global research showing that carnivores are often perceived as major threats to livestock [7]. Human–wildlife conflict is a pervasive conservation challenge, particularly in biodiversity hotspots where carnivores coexist with humans [14–16]. These conflicts often lead to significant socio-economic losses for rural communities. In areas where wild prey compete with livestock for resources, their decline has exacerbated human–wildlife conflict through livestock predation [32,59]. Ecological, socio-economic, and cultural factors drive these conflicts, with habitat depletion and prey depletion increasing livestock predation risk [18,60]. Globally, large carnivores such as lions, jaguars, pumas, and hyenas conflict with humans, resulting in retaliatory killings and declining populations [17]. These carnivores impose significant economic losses on rural communities [39,61]. In some regions, livestock constitute up to 70% of carnivore diets, leading to economic losses of USD 50 to 300 per household annually.

Conversely, wild boars were predominantly categorized as negligible threats to livestock but were held solely responsible for crop damage. This dual perception underscores the species-specific nature of human–wildlife conflict, where carnivores are linked to livestock predation and omnivorous species like wild boars are associated with crop destruction. Wild boars frequently damage crops and property, resulting in substantial economic losses [9,10,22,23,62]. Their omnivorous diet includes over 400 plant species, among which 40 are staple crops [33]. They damage agrarian lands, orchards, forests, pastures, and nurseries, destroying crops at all growth stages, from seedlings to mature plants [63]. The high reproductive rate, generalist diet, and lack of natural predators that enable rapid population growth have heightened the scale of agricultural damage, significantly contributing to food losses among farmers and intensifying HWC [64]. Additionally, the damage inflicted by wild boars contributes to a more negative public perception of wildlife [5]. Every year, rural communities bear substantial economic losses due to wild boars [65].

In addition, we found that wild boars raid farmlands predominately at night and during certain seasons (autumn and spring seasons) (see Section 3.4: "Temporal and Seasonal Patterns in Crop Raiding and Damage" for details). These patterns reflect the availability of preferred crops, such as maize and wheat, during this season. In particular, maize was the crop most frequently targeted, a finding consistent with other studies [66,67]. Seasonal and nocturnal crop-raiding behaviors are well documented in wild boar populations, as they exploit agricultural fields during harvest seasons when crop density and nutritional value are highest [68,69].

The economic analysis revealed that wild-boar-driven economic losses due to crop damage were significantly higher than other losses (livestock predation or poultry losses) attributed to other predators (see Section 3.5: "Predation Patterns and Economic Impact of Species" for detail). These findings align with studies that identify wild boars as one of the most destructive wildlife species for crops globally [66,70]. The annual economic losses reported in this study, particularly from wild boar crop damages, represent a significant financial burden for affected families. The annual losses due to wild boars exceed the average rural household income in Khyber Pakhtunkhwa [71,72]. These losses are notably higher than those reported in other studies [73,74], highlighting the severity of human–wildlife conflict in general, specifically emphasizing the impact of wild boars in the area.

The study area experiences minimal livestock losses from carnivores like grey wolves and golden jackals, likely due to their low population and sighting rates. In contrast, wild boars are abundant and highly adaptable, thriving in various environments and frequently raiding crops near farmlands. The agrarian nature of the region, with cropland often intersecting natural habitats, further increases the risk of wild boar crop damage. Addition-

ally, locals maintain small, well-managed livestock herds, typically housed securely with adequate fodder, reducing vulnerability to predation. While proper livestock management helps mitigate predation risks, the lack of fencing leaves crops unprotected from wild boar raids, making crop losses significantly higher than livestock losses in the area.

The findings of this study contribute significantly to the broader understanding of human–wildlife conflict (HWC), particularly in rural, agriculture-dependent communities. While our research is based in District Lakki Marwat, Pakistan, it aligns with global trends in HWC, where communities experience significant economic losses from crop damage and livestock predation. Similar conflicts have been documented in other rural areas worldwide, particularly in regions like Europe and Asia, where species such as wild boars and large carnivores, like wolves and hyenas, cause significant agricultural and livestock losses [23,75,76]. These findings underscore the global nature of HWC and highlight the need for integrated, context-specific management strategies that can be adapted to diverse agro-pastoral landscapes [77,78].

The analysis of community attitudes highlights the polarized perceptions of wildlife species. Wild boars were viewed most negatively, with over 70% of respondents advocating for their elimination (see Section 3.6). Grey wolves and striped hyenas also received moderate negative perceptions due to their impact on livestock. Negative attitudes were significantly associated with economic losses, specifically caused due to crop damage, for which wild boars were held responsible. This explains the highest prevailing negative attitude toward wild boars in the area. As in our study area, the majority of the losses were due to crop damage, while losses due to other species (carnivores) were negligible. The results are consistent with studies demonstrating that economic losses intensify negative attitudes toward wildlife and drive retaliatory actions [79–82].

The intensity of human wild boar conflict is likely to escalate in the region, with the reconstruction and reopening of the Marwat Canal [83]. This development would enable locals to cultivate long-abandoned agricultural lands previously left unused due unavailability of a consistent water supply. The canal will enhance irrigation activities, leading to an expansion of wheat and maize cultivation in the area. As the sowing area increases, the risk of crop damage will rise, potentially escalating human–wild boar conflict. These crops are highly attractive to wild boars, whose population thrives in the area due to the presence of natural dens and species habitat (first author's personal experience).

Protecting crops from wild boar raiding necessitates devising different management strategies. Physical barriers, like electric fencing, are considered the most effective deterrent, causing a mild, non-lethal electric shock to deter wild boars from raiding the crop. Building non-electric fences or trenches around the agricultural land could also work as an effective barrier against wild boars' intrusion. Other electronic deterrents, including lights, sound alarms, or sprinklers, offer a dynamic approach by discouraging boars during nighttime. In addition to non-lethal methods, sanctioned lethal control measures, when necessary and legally approved, could serve as a last resort for managing severe wild boar infestations, provided they meet regulatory requirements. However, such measures are typically only implemented when other management strategies prove ineffective.

Additionally, crop rotation and planting of less-preferred crops in high-conflict land during peak foraging times may lessen the crop damage and associated economic losses. Employing a combination of these strategies would help protect crops while fostering coexistence between wild boars and agricultural communities [84]. Therefore, site-specific management strategies, such as combining physical barriers with active deterrents, are crucial for mitigating wild boar damage effectively. Additionally, collaborative efforts between local communities and conservation authorities are essential to enhance the effectiveness of these methods. Information sharing and technical support for implementing innovative

solutions can help farmers adapt their strategies over time. These measures, alongside tailored approaches like crop rotation or planting less palatable crops near high-risk areas, offer a sustainable pathway to reducing economic losses caused by wild boars [85]. The findings underscore the need for tailored conflict mitigation strategies. For wild boars, measures such as community-based deterrents, fencing, and seasonal crop rotation could help reduce crop damage [86]. Given the socio-economic vulnerabilities of smallholder farmers, compensation schemes or financial incentives for adopting non-lethal control methods could foster coexistence.

This study highlights the socio-economic challenges of HWC in rural Pakistan, emphasizing the dual need to protect livelihoods and conserve wildlife. Community engagement is crucial for developing sustainable conflict mitigation strategies. Participatory approaches that integrate local knowledge and involve stakeholders in decision-making can enhance the effectiveness of conservation efforts [87,88]. Additionally, addressing underlying drivers of conflict, such as habitat degradation and prey depletion, is essential for reducing human–wildlife interactions and fostering coexistence.

5. Conclusions

This study provides a comprehensive assessment of human–wildlife conflict (HWC) in the rural communities of northwestern Pakistan, focusing on both carnivorous and omnivorous species. Unlike conventional narratives that emphasize carnivores as the main drivers of conflict [18,31,37–39], our findings highlight that negative community perceptions are largely shaped by the economic impact of a species, rather than ecological role or feeding behavior. The disproportionate hostility toward wild boars, despite their non-predatory nature, underscores the need for mitigation strategies tailored to the economic realities of affected communities. Unlike carnivore conflict, which often centers on livestock predation, wild boar-related losses are predominantly linked to crop damage, requiring a different management approach. The findings underscore the need for a multi-pronged approach, combining traditional deterrents, and advanced methods such as game-proof fencing, trenches, bio-fencing, crop rotation, and watchtowers combined with group vigilance and community-based initiatives to reduce crop and livestock losses. Integrating these methods with education campaigns, habitat management, and government-supported compensation schemes can significantly mitigate conflicts. Beyond direct conflict mitigation, this study also highlights an unintended but valuable outcome: by engaging with local communities, the research itself fostered discussions on the ecological role of wildlife, encouraging greater awareness of conservation issues. Comprehensive field surveys, including camera trapping and sign surveys, are recommended to assess the status of the observed species in the area. Addressing these conflicts holistically is critical for fostering coexistence and ensuring the sustainable management of biodiversity in the region.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d17030180/s1: Table S1: Consent letter used in this study; Table S2: Questionnaire used in this study; Table S3: Perceived danger of the species as a threat to livestock; Table S4: Temporal and seasonal patterns of crop raiding events; Table S5: Wild boar-induced crop damage: reported losses in Pakistani Rupees (PKRs) and United States Dollars (USDs); Table S6: Community attitudes toward species populations. The percentage distribution of attitudes highlights the dominance of particular attitudes across species.

Author Contributions: Conceptualization: T.U.K. and H.H.; methodology: T.U.K., A.I., K.U. and G.N.; software: T.U.K., K.U. and A.I.; validation: T.U.K., K.U., H.H. and A.I.; formal analysis: T.U.K.; investigation: T.U.K., K.U., A.I. and G.N.; resources: H.H.; data curation: T.U.K., A.I., K.U. and G.N.; writing—original draft preparation: T.U.K.; writing—review and editing: H.H., K.U., A.I. and G.N.; visualization: T.U.K. and A.I.; supervision: H.H.; project administration: T.U.K., G.N., K.U.

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Conflicts of Interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Abbreviations

The following abbreviations are used in this manuscript:

HWC	Human–wildlife conflict
PKR	Pakistani Rupee
USD	United States Dollar
km	Kilometer

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A Game of Risk: Human Activities Shape Roe Deer Spatial Behavior in Presence of Wolves in the Southwestern Alps

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Abstract: In human-dominated landscapes, human activities shape prey spatial behavior, creating complex landscapes of risks. We investigated habitat selection of roe deer using resource selection functions in a human-dominated mountain system located in the southwestern Alps, characterized by a high presence of wolves and human disturbance. Our study aimed to assess how the interplay of hunting, presence of infrastructures, and recreational activities in the presence of wolves influenced roe deer spatial responses inside and outside a protected area. We documented that during the hunting period, roe deer increased selection of high-wolf-density areas, with the strongest effect observed during wild boar drive hunts, supporting the risk enhancement hypothesis, where avoiding one predator increases exposure to another, and highlighting the temporary yet significant impact of hunting on predator–prey dynamics. During the period of the wild boar drive hunt, roe deer also showed stronger selection for proximity to buildings, supporting the human shield hypothesis. Protected areas had an increased effect on roe deer avoidance of trails, where hiking and recreational activities are more concentrated. Our findings revealed the complex trade-offs that roe deer face in navigating multiple risks within human-modified landscapes, important for the development of effective conservation and human sustainability strategies.

Keywords: human disturbance; landscape of fear; human shield; risk enhancement; human–wildlife interactions

1. Introduction

Anthropogenic use of the landscape has substantially restructured natural ecosystems, causing not only habitat loss and fragmentation [1], but also species declines as well as changes in the interactions among species [2,3]. Humans and their activities have assumed an important role in shaping ecological communities [4,5], introducing additional complexity to the relationships between predators and prey [6]. Wildlife increasingly faces the challenge of navigating human-altered environments [1], with animals adapting in various ways to the presence of human activities [7,8]. Beyond inducing direct wildlife mortality, human activities such as hunting, land modification, infrastructure development, and recreational use reshape landscapes of fear in ways that can affect habitat selection and activity patterns of prey and predators, as well as antipredator behaviors [9,10].

Ungulates have to navigate spatiotemporal risks from both humans and natural predators in heterogeneous habitats [11]. In the case of highly anthropized environments, the complexity of the interplay of human–prey–predator interactions is exacerbated. Prey avoiding one risk might increase their vulnerability to another, a phenomenon known as

risk enhancement [12,13], or prey may select for proximity to human features as a shield to minimize risk [14]. Wildlife species respond to human activities in complex spatial ways, influenced by the type, intensity, and frequency of disturbance [15,16], as in the case of recreational activities or hunting.

Hunters employ specific strategies to optimize hunting efficiency, which interact with different habitat characteristics and anthropogenic features within the landscape and affect prey spatial behavior [17,18]. Hunters typically rely on different approaches depending on the target game species but are generally restricted to daylight hours and specific periods over the year. Human linear features, such as roads and trails, create additional risks to wildlife also by intensifying human access to remote areas, which may indirectly alter species interactions [19]. These features are also used for various types of recreation, ranging from activities such as hiking and biking to motorized activities [20]. Non-consumptive outdoor recreation can have significant behavioral effects on wildlife, including ungulates, through spatial avoidance [21], increased movement speeds [22], or shifts in diel activity patterns [23]. For example, in a study on red deer and sheep interaction, both species were more likely to be detected further from the path during the day, suggesting that hiking pressure influenced spatio-temporal interactions [24]. Outdoor activities like hiking and biking also induced avoidance responses in wapiti [25,26] and chamois, with higher intensity in popular recreational areas, such as natural protected areas [27]. In other cases, human infrastructures have been used by prey as shields to predation risks [14,28]. Hence, in human-dominated landscapes, there is a need to understand the complexity of the spatial interactions of prey, natural predators, and human activities to allow management decisions that optimize long-term sustainability.

Our study investigates the spatial interplay of the effects of human disturbance and predator presence on roe deer spatial behavior, inside and outside a natural protected area. Roe deer provides an excellent model species for studying these dynamics, given that it is widely spread and abundant in Europe [29–31] and in the area of study [32], where it is the main hunted species for both hunters and wolves [33], and demonstrates high tolerance and plasticity for anthropogenic disturbances [34]. By quantifying the spatial and temporal effects of combined human activities and wolf presence spatial risks, we aim to investigate how spatial variation in human disturbance, arising from both recreational activities and hunting, affects roe deer habitat selection in and outside a protected area, providing key insights for conservation and wildlife management in heavily human-impacted landscapes.

2. Materials and Methods

2.1. Study Areas and Data Collection

The study area was located in a mountainous region in the southwestern Alps, Italy (44°21′ N, 7°66′ W in EPSG:4326, WGS84) (Figure 1), ranging in elevation from 270 to 2160 m. The landscape is predominantly forested (59%, mainly deciduous), with open habitats (12%) and urbanized areas (29%). Part of the study area lies within the Marguareis Natural Park (PNM, 80.4 km^2), where ecotourism is highly developed and actively promoted. Hunting is prohibited within the protected area, while outside it is regulated by national law within a Hunting District following the guidance documents of the Regional Administration of Piedmont (Figure 1a). Between September and January, two main game species are hunted: wild boar, primarily through collective drive hunts, and roe deer, with single hunters using a sit-and-wait strategy. Roe deer, reintroduced into the study area in the late 1980s for both hunting and conservation purposes, are now widely distributed throughout the region. Wild boar began recolonizing the area in the 1990s. Roe deer were documented to be the most frequently recorded ungulate species on a simultaneous camera trap study conducted

in the same area [32], with an estimated occupancy of 0.91 (SE = 0.03) over 56 sites [35], which indicates their wide distribution.

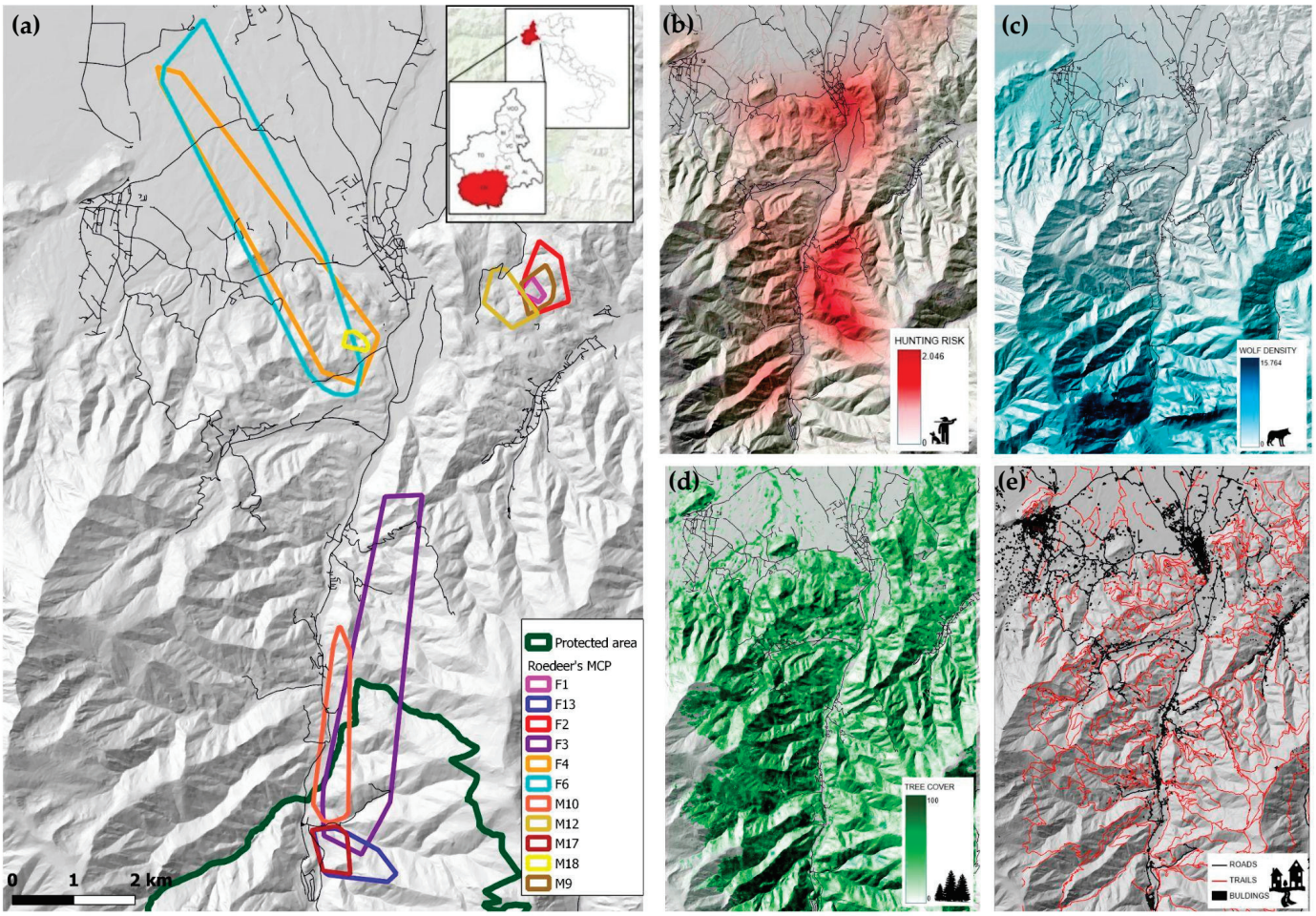

Figure 1. Description of the study area: site location and spatial distribution of roe deer home ranges (Minimum Convex Polygons, MCPs) within the study area (**a**). On the right, inset maps showing (**b**) hunting risk density (range: 0–2.046), (**c**) wolf density (range: 0–15.764); [36], (**d**) tree cover density (range: 0–100), and (**e**) the distribution of roads, trails, and buildings within the study area.

The study area is characterized by a medium-to-high level of rural urbanization typical of lower-altitude landscapes, with small villages, roads, and a dense network of trails. The region also hosts the higher density of wolves documented in the Italian Alps [36], which have been present since 1996 [37] through natural dispersals [38].

We used data from Global Positioning System (GPS)-collared roe deer to investigate habitat selection. Roe deer were captured throughout the study area during winters 2022–2024 using individual box traps with trap alarm systems, specifically built for this study based on roe deer local sizes and logistical needs to guarantee the safest capture method, commonly used for roe deer in other areas with severe winters [39] and efficient in terms of timing in responsiveness of the team intervention (20–30 min) [32]. Box traps were distributed in the study area to capture roe deer both in and outside hunting areas, and in areas with different gradients of anthropization disturbances, variables which are particularly important to represent in the study. No chemical immobilization was needed [32]. Roe deer were fitted with GPS collars (model Lotek Litetrack Iridium 360, Lotek Wireless, Newmarket, ON, Canada). Collars were programmed to attempt a fix at least every 7 h. GPS locations were screened for GPS errors or malfunctions, and only fixes with a level of accuracy of PDOP < 5 were considered. A systematic GPS collar test

of the Lotek collar's performance was conducted in the different parts of study area to guarantee the homogeneity of the accuracy of the Positional Dilution Of Precision (PDOP): information acquired in the different areas [32]. We investigated roe deer habitat selection over a 7-month period to test for the effect of hunting, encompassing 3 typical distinct periods: (a) before the hunting season (1 August–15 September), (b) during the hunting season (hunting season started on 16 September and ended 31 December), and (c) after the hunting season (1 January–28 February). The hunting season was further characterized by two distinct periods: (1) "Roe deer hunt" in September–October, where hunting primarily targeted roe deer through a sit-and-wait hunting strategy, and (2) "Wild boar hunt" in November–December, when hunting activity was predominantly focused on wild boar through drive hunts.

In total, our dataset consisted of GPS telemetry data from 11 individuals, containing 7433 locations.

2.2. Anthropogenic and Environmental Covariates

We studied the influence of distinct environmental and anthropogenic covariates on roe deer habitat use, hypothesizing that these variables are correlated with spatial patterns of perceived risk or disturbance from humans and wolves (details of every covariate in Table S1 (Supplementary Table S1)). Environmental covariates included tree cover density (*tree cover*), representing the percentage of vegetation cover at each GPS point, derived from the Tree Cover Density layer using QGIS 3.34.6. The covariate has a high resolution of 10 m and was sourced from the Copernicus Land Monitoring Service (EAA Copernicus, https://land.copernicus.eu/en) (accessed on 1 march 2023). We evaluated this variable to test the hypothesis that forest might provide roe deer with refuge or increased opportunities to escape from predators, hunters and any human disturbance such as hikers or bikers.

Anthropogenic features included roads (all paved roads), trails (all unpaved paths), and buildings (all types of human dwellings) and were obtained by BBBIKE (https://extract.bbbike.org/) (accessed on 15 march 2023) from OpenStreetMap (OSM). For each of these covariates, we calculated the minimum Euclidean distance from each GPS point to the corresponding feature, resulting in the variables *dist.road*, *dist.trail*, and *dist.build*. We evaluated these variables to test for the hypothesis of human disturbance, considering in particular that roads are regularly used by people with motorized vehicles, whereas trails are used by hikers and bikers, and in general by recreational tourism in the study area [40,41].

To test for hunters encountering risk, we considered the georeferenced harvest data provided by hunter districts from 2016 to 2024 (n = 1281), and applied a 95% kernel density estimation to quantify the spatial density of hunted animals, using the R version 4.3.1, package *amt* [42] to generate a hunting risk map with a spatial resolution of 10 m, which was then scaled from 0 to 1 (huntrisk). We account for local wolf density of presence (*wolfden*), using the wolf density map estimated by Marucco et al. 2023 [36] for the whole Italian Alps based on a spatial capture–recapture model fitted to the noninvasive genetic data collected in winter 2020–2021.

To test how human activities affect resource selection of roe deer in relation to hunting periods we created two categorical temporal variables named "*Hseason1*" and "*Hseason2*". In *Hseason1*, we classified the study into the 3 periods previously described: *Before* (no hunting activity), *During_hunt* (period with active hunting), and *After* (post hunting period). In *Hseason2*, we further distinguished the hunting period into two distinct phases based on the type of hunting activity, named "*DuringROE_Hunt*" and "*During WB_Hunt*", as previously described. This variable categorization is meaningful to test the hypothesis of spatial responses to different hunting methods: roe deer hunting relies on a sit-and-wait

mode, involving a single hunter either actively searching for animals or waiting passively in a specific location, while wild boar hunting relies on a drive hunt mode with a team of hunters working together with dogs to locate and stalk animals. The driving hunt mode is generally considered more disruptive due to the involvement of multiple hunters and dogs, which increase noise and movement across the landscape [43,44]. To test how spatial responses changed with hunting periods, we included interactions between *Hseason1 and Hseason2* and the most significant predictors (Table 1). Hence, the 2 variables *Hseason1 and Hseason2* allowed us to investigate the general effects of hunting risk and the specific impacts of different hunting strategies, respectively.

Table 1. Tested hypotheses, corresponding variables, and predictions of roe deer spatial response in anthropogenic landscape (interaction terms are expressed using "×" between the variables).

Hypothesis	Variables	Predicted Effect	Predictions
H1: Forest cover is an important refuge habitat in an anthropogenic landscape	*tree cover*	(+)	Roe deer is a woodland species with preference for ecotonal zone [45] P1: In an anthropogenic landscape, we predict that tree cover density may be important as a refuge area
H2: Spatial effect of recreational activity	*Dist.trail*	(+)	P2a: Roe deer may avoid trails used by hikers and bikers as recreational activities to minimize perceived risk from human disturbance
	Dist.trail × *InsidePA*	—	P2b: We predict roe deer avoidance of trails should be greater within the Protected Area where tourism is more concentrated
H3: Effects of pre–during–post hunting periods, and human shield strategy	*Huntrisk*		P3a: Roe deer habitat selection may be affected by the spatial presence of hunting activity
	Dist.build × *Hseason1*		P3b: stronger use of a human shield strategy during the hunting period than before (or after)
H4: Effects of different hunting modes	*Hseason2 vs. Hseason1 as temporal interaction terms*		Roe deer may exhibit varying responses depending on the distinct hunting practices. P4: Specifically, we predicted that wild boar hunting may have a greater impact due to the higher levels of disturbance associated with this activity. During the wild boar hunting period, we anticipate a stronger use of the human shield strategy
H5: Risk enhancement	*huntrisk* × *wolfden*	(+)	P5a: Roe deer may select areas where both risks are high simultaneously (cumulative exposure)
	huntrisk × *wolfden*	(−)	P5b: Roe deer, avoiding one predator, may select areas where the other predator is more common

The spatial categorical variable, named *InsidePA*, allowed us to test the hypothesis of a higher effect of recreational activities within the protected area, where tourism is more

developed, specifically along trails. To test this hypothesis, we tested the interaction effect between *trail* and *InsidePA* (Table 1).

2.3. Resource Selection Function and Analytical Framework

We evaluated roe deer habitat selection building third-order resource selection functions (RSFs). RSFs evaluate the habitat features selected by animals by comparing used locations to available locations within the domain of availability, defined here as each individual roe deer's home range (third-order habitat selection, Johnson 1980). Individual home ranges were defined as the area encompassing 95% of the kernel density estimates estimated by the 'amt' package in R version 4.3.1 [42] and were calculated using roe deer GPS data collected between 1 August and 29 February 2022–2024. To characterize habitat availability within the home range, we considered 30 random locations for each GPS fix [46]. RSF parameters have been estimated using a Generalized Linear Mixed Model (GLMM) using glmmTMB package in [47], based on a mixed-effect logistic regression model for binary data for used locations (1) and random locations (0), and setting a random intercept for each individual to account for the non-independence of observations of a given roe deer and the unbalanced sampling design [48,49]. The general form of the model is as follows:

$$\text{logit}\,(p) = \beta 1X1 + \beta 2X2 + \ldots. \beta iXi$$

where p is the probability of selection, the x_is are the explanatory covariates or interactions, and β_i is their respective coefficient. Temporal covariates for *Hseason1 and Hseason2* entered the models only via their interactions with spatial covariates.

We built our RSF candidate models based on our specific hypothesis (Table 1). Before initiating the stepwise modeling process based on the delineated hypothesis, we screened for redundancy among predictors by calculating Pearson's correlation coefficients (r) using the cor() function in R. Variables with $r > 0.7$ were not included in the same model to prevent collinearity issues. To analyze the effect of independent covariates, we began by testing the effect of habitat and anthropogenic features first, then added risk variables, such as wolf density (*wolfden*) and hunting risk (*huntrisk*), without any interaction terms. Then, we sequentially added variables and interactions to test for specific hypotheses as indicated in Table 1, and identified the most significant predictors driving roe deer habitat selection across environmental, anthropogenic, and risk gradients, ensuring a robust and interpretable modeling framework.

The candidate models were ranked using the Akaike Information Criterion (AIC; [50]) and all the models were additionally checked for any multicollinearity using the Variance Inflation Factor (VIF) function of the package car, with a correlation threshold of 5 being applied or at least less than 10 only in case of the interaction term [51].

3. Results

The best models include interactions with the temporal covariate that considers the hunting periods and modes (*Hseason2*) and with the spatial covariate *InsidePA* (inside/outside the protected area), confirming that roe deer habitat selection is primarily explained by the complex interplay of multiple anthropogenic factors. In particular, the most parsimonious RSF model (M1, lowest Δ AIC, Table 2) explains the majority of the variance of the data (weight of 0.92) and included key predictors both in the form of a single covariate effect and their interactions (Table 2 and Figure 2).

Table 2. Summary of best candidate RSF models investigating the habitat selection of 11 roe deer before, during, and after the hunting season in the Pesio Valley, Maritime Alps.

Mod	Formula	Δ AIC	*W*
M1	~treecover + dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.build:Hseason2 + huntrisk:wolfden + dist.trail:InsidePA	0	0.92
M2	~treecover + dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason1 + dist.build:Hseason1 + huntrisk:wolfden + dist.trail:InsidePA	4.9	0.08
M3	~treecover + dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.build:Hseason2 + huntrisk:wolfden	46.8	0.00
M4	~treecover + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.build:Hseason2 + huntrisk:wolfden	73.2	0.00
M5	~treecover + dist.trail + dist.build + wolfden:Hseason2 + dist.build:Hseason2 + dist.trail:InsidePA	166.6	0.00
M6	~treecover + dist.trail + huntrisk + wolfden + huntrisk:wolfden + dist.trail:InsidePA + dist.road	305.7	0.00
M7	~treecover + dist.trail + wolfden + huntrisk + wolfden:Hseason2 + dist.trail:InsidePA + huntrisk:wolfden	311.8	0.00
M8	~treecover + dist.trail + huntrisk + dist.trail:InsidePA + huntrisk:wolfden	348.9	0.00
M9	~dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.trail:InsidePA + huntrisk:wolfden + dist.build:Hseason2	472.1	0.00
M10	~treecover + dist.trail + dist.build + wolfden + huntrisk	90,176.2	0.00
M11	~treecover + dist.trail + dist.build + wolfden	90,206.6	0.00
M12	~treecover + dist.trail + dist.build	90,287.9	0.00
M13	~dist.trail + dist.build	90,357.8	0.00

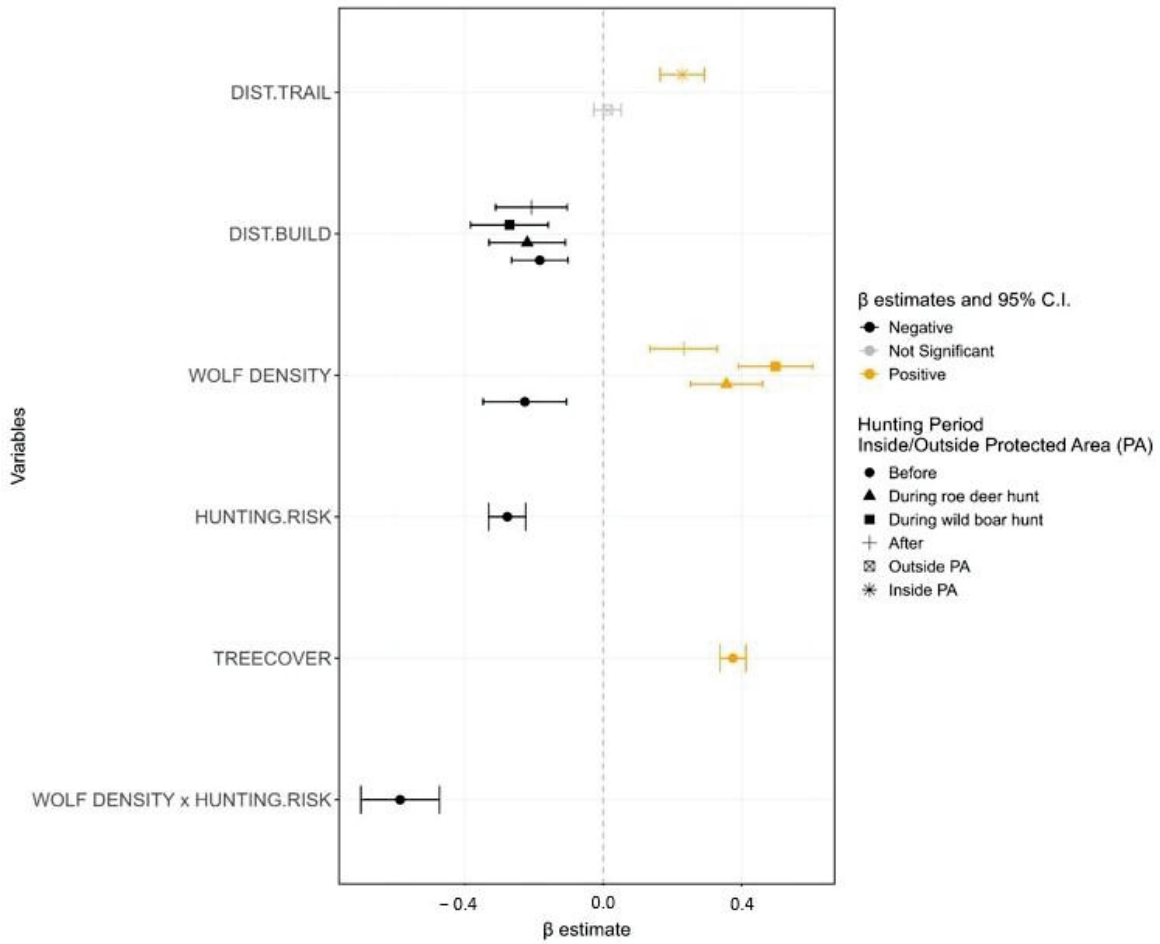

Figure 2. β coefficient plot of fixed terms (expressed as log-odds ratios) included in the most parsimonious model. The dashed line represents a level of use proportional to availability, and error bars represent 95% confidence intervals. The timing effect for each variable is indicated by different symbols: dots (before), triangles (during roe deer hunt), squares (during wild boar hunt), and crosses (after hunting period). The spatial effect of *dist.trail* is shown with striped squares and asterisks, representing coefficients for locations outside and inside the park, respectively. β coefficients are displayed in black if negative, orange if positive, and gray if not significant.

Tree cover density emerged as one of the most significant predictors: removing this variable from the model caused a notable decline in model performance, with the best model shifting from first (M1) to ninth (M9) (Table 2). Roe deer selected for high cover density, as indicated by the positive effect of tree cover covariate ($\beta = 0.37$, SE = 0.019, $p < 0.001$), testing for H1. Trails had no significant effect on roe deer habitat selection ($\beta = 0.01$, SE = 0.02023, $p = 0.541$). However, roe deer significantly avoided trails within the protected area, as indicated by the positive coefficient of the interaction term *dist.trail:InsidePA* when *InsidePA* = 1 (Figure 3 green line, $\beta = 0.23$, SE = 0.03252, $p < 0.001$), testing for H2.

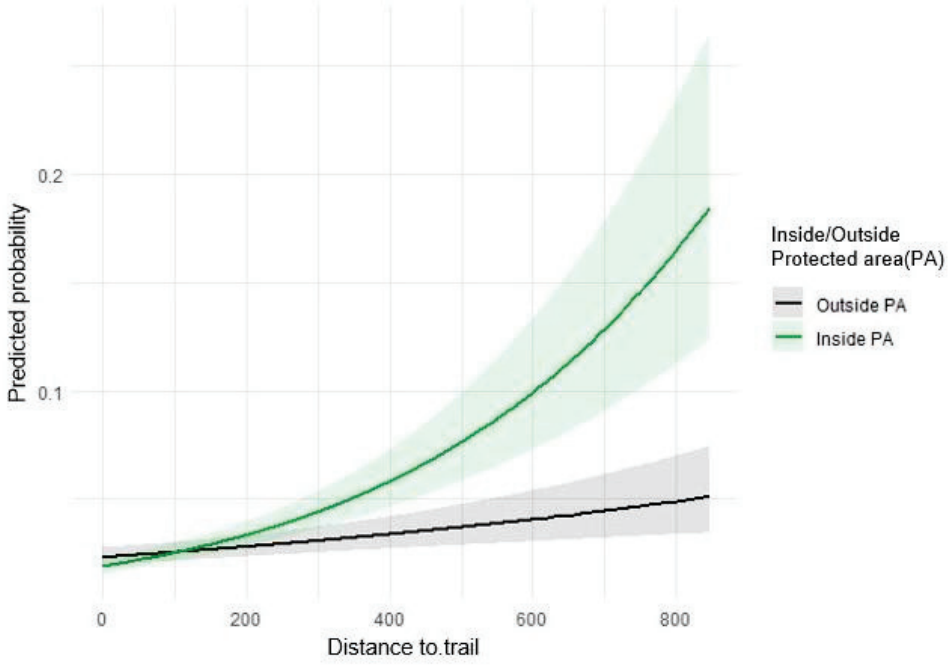

Figure 3. Predicted probability of trail use by roe deer inside (green line) and outside (black line) the protected area.

We observed a general avoidance of high-risk areas associated with hunting, as indicated by the negative main effect of *huntrisk* ($\beta = -0.28$, SE = 0.02725, $p < 0.001$), and a clear temporal effect of hunting on roe deer spatial responses, testing for H3 and H4. This temporal effect is better explained by considering the different hunting periods and modes (*Hseason2* in best model M1) rather than just the presence or absence of hunting (*Hseason1* in M2, Δ AIC = 4.9), testing H4. During the hunting season, roe deer responses to wolf density and proximity to buildings were influenced by the different temporal periods of hunting activities (Figure 4). Roe deer selection for proximity to buildings (dist.build) was consistently negative ($\beta = -0.18$, SE = 0.04162, $p < 0.001$), but increased over the hunting periods with the interaction term (*dist.build:Hseason2*), particularly during wild boar hunting, where the coefficient was higher compared to other periods ($\beta = -0.27$, SE = 0.05742, $p < 0.001$). This effect persisted after the hunting season ended ($\beta = -0.21$, SE = 0.05288, $p < 0.001$), although it was less pronounced, testing for H3b (Figure 4b).

The negative main effect of wolf density (wolfden), which reflects the effect in the absence of hunting, indicates that roe deer tend to avoid areas with high wolf presence ($\beta = -0.23$, SE = 0.06147, $p < 0.001$); moreover, there is a significant negative effect of the interaction term *wolfden:hutrisk* ($\beta = -0.59$, SE = 0.05798, $p < 0.001$), which indicates that roe deer, avoiding areas with risk from one predator, selected areas with high risk for the other (Figure 4a). In particular, roe deer responses to wolf presence changed within the different hunting periods: roe deer shifted their response from avoidance of wolf areas of presence before the hunting period to a selection of those areas during hunting, testing

H5 (Figure 4a). The selection was particularly strong during wild boar hunting (β = 0.50, SE = 0.05485, $p < 0.001$) and less pronounced during roe deer hunting (β = 0.36, SE = 0.05315, $p < 0.001$). After the hunting season, the effect diminished but remained positive (β = 0.23, SE = 0.04958, $p < 0.001$) (Figure 4a).

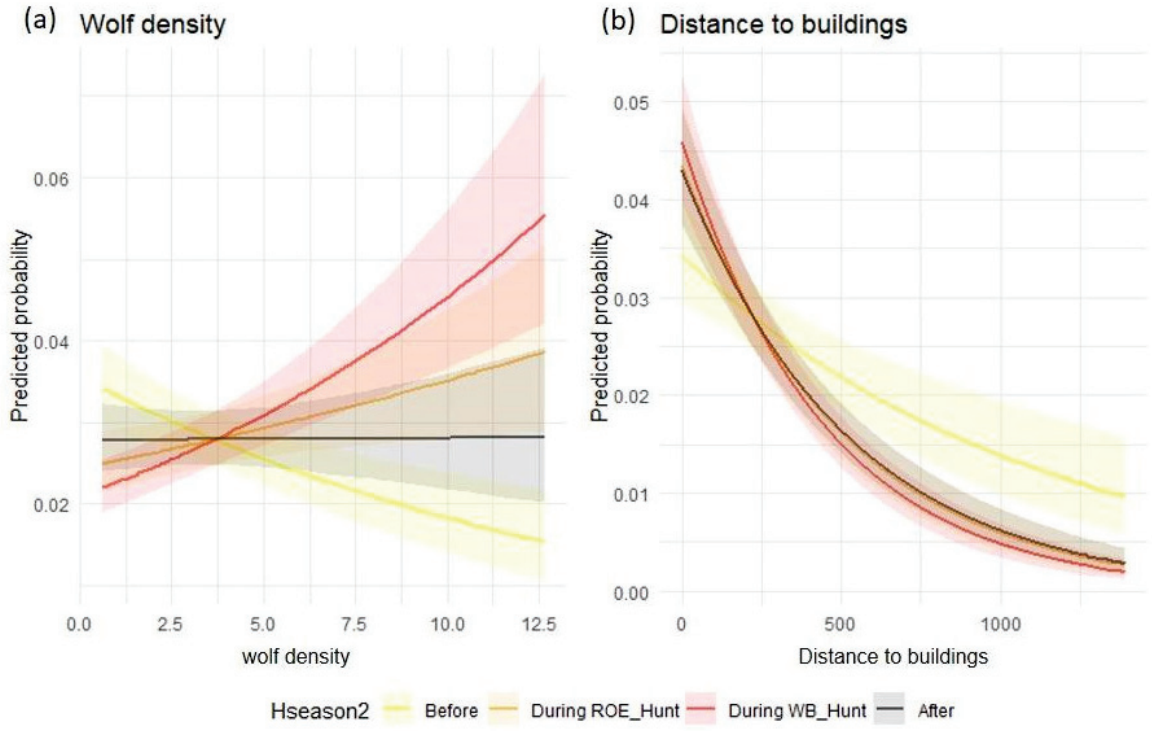

Figure 4. Predicted probability of habitat use by roe deer based on wolf density (**a**) and distance to buildings (**b**) across different temporal periods: Before, prior to the hunting season; During_ROE_Hunt, the first hunting period characterized by roe deer hunting; During_WB_Hunt, the second hunting period characterized by wild boar hunting; and After, following the closure of the hunting season.

4. Discussion

Human activity has significantly transformed natural ecosystems, shaping the composition and structure of ecological communities, and leading to alterations in species interactions [1,2]. This influence introduces additional layers of complexity into predator–prey relationships, often challenging the natural dynamics of these interactions. Hence, behavioral adaptations in the Anthropocene, such as changes in habitat selection or temporal activity, are important for the resilience of some species [7,52–54]. However, not all species can adapt successfully, leading to uneven impacts of disturbance across ecological systems. Few studies have explored ungulate responses to cumulative landscape disturbances involving multiple risks [55]. In this paper, we have investigated how human activities influenced roe deer habitat selection in relation to hunting, human infrastructures, and recreational activities in the presence of its most important natural predator, the wolf. We included random intercepts for individual ID in all our models, as recommended by Gillies et al. (2006) and Merrill and Hebblewhite (2009) [48,49], to account for differences in sample size per individual and controls for individual-specific effects in habitat selection. Our findings highlighted that human activities play a crucial role in shaping roe deer habitat selection strategies, in particular the timing and type of hunting and the distribution of trails and buildings, providing important insights into these complex spatial and temporal dynamics. Human-induced alterations and disturbances transform what ecologists refer to as "landscapes of fear" [56]. These landscapes influence how animals perceive and

respond to threats in their environment driving critical behaviors [15]. Human activities might reshape the landscapes of fear, influencing habitat selection, activity patterns, and the effectiveness of anti-predator strategies [10,52] such as introducing "human shield strategies" [14]. In our study, we had the unique opportunity to investigate in detail how roe deer navigate a highly heterogeneous "landscape of fear" induced both by human disturbances and the presence of a natural predator, where risks varied both temporally and spatially. In particular, during the hunting season, roe deer were demonstrated to face intensified trade-offs, as human hunting activity overlapped in space and time with predator presence and all the other human pressures. At the same time, part of our study area is in a protected area, which experiences high levels of tourist activity throughout the year, especially along trails. Our results revealed that the combined pressure of anthropogenic infrastructures and variegated human activities, along with the presence of wolves, prompted roe deer to adopt differentiated strategies to balance their exposure to threats. This adaptive response is supported by the fact that roe deer behavior aligns with multiple hypotheses we predicted (from H1 to H5) rather than being explained by a single one. This suggests a complex interplay of various factors and strategies employed by this prey species in a highly anthropogenic context.

We documented strong support for our first hypothesis that tree cover density was one of the most significant drivers of habitat selection (H1). As a woodland and ecotonal species, roe deer rely on forested areas to ensure immediate escape routes [51,57]. Benhaiem et al. (2008) [58] showed that vigilance levels in roe deer decreased commensurately with the extent of woodland, further highlighting the role of forest cover in reducing perceived risk. This indicates a general adaptation of roe deer to the highly anthropogenic landscapes of our study area, where human pressures, combined with the presence of natural predators, create a complex landscape of risk, requiring prey to optimize their spatial strategies by using refuge areas more extensively. This finding also emphasizes the need to reconsider methodologies for ungulate population estimates in anthropized contexts that rely only on direct observations [59,60], which may be strongly affected by low and unpredictable detection rates [61]. Based on our findings, anthropogenic pressures might drive roe deer to increasingly select forested refuge areas, where detection rates are likely too low for direct observations to serve as methods for reliable population estimations.

Among human linear features, trails had the strongest effect on roe deer habitat selection. We hypothesized that deer would perceive these features as risky, due to their frequent use by hikers, bikers, and humans in general, especially where tourism is more concentrated (H2). In fact, we found support for our hypothesis (P2b) where roe deer displayed stronger avoidance of trails inside protected areas compared to outside them. This heightened avoidance within the protected area is likely influenced by the higher frequency of tourists and recreational activities inside the park. The rapid spread and diversification of outdoor recreation can impact wildlife in various ways, often leading to the avoidance of disturbed habitats [62,63]. Also, Mathisen et al. (2018) [64] showed that hiking and cycling activities on trails reduced deer space-use and browsing on tree saplings in their direct vicinity (<100 m).

Our results aligned with hypotheses H3 and H4, demonstrating that hunting periods modify roe deer habitat selection strategies. Roe deer change spatial behavior during the hunting season compared to a previous period characterized by the absence of hunting through an increased selection for proximity to buildings, particularly during the wild boar drive hunting period. Also, other studies have shown that drive hunting is particularly disruptive to wildlife [43]. This supports the hypothesis that roe deer use human buildings as refuges from hunting activities, indicating a well-developed human shield strategy [28]. Particularly interesting is also the effect of hunting activities on the relative use of areas

with higher wolf densities. The β coefficients of wolfden shifted from negative before the hunting season to increasingly positive during the hunting season, peaking during the wild boar hunting period, and then returning to neutral immediately afterward. This clear temporal pattern (Figure 4a) highlights how hunting activity can play an important role in prey–predator interactions, likely driving both species to converge in the same remote areas, indicating that roe deer might not actively select high-wolf-density areas per se, but rather select locations characterized by refuge areas, which are also typically selected by wolves [65,66].

Additionally, as predicted in our risk enhancement hypothesis (H5), we found a negative interaction between hunting risk areas and high-wolf-density areas, suggesting that roe deer actively avoided areas where risks from both hunters and wolves overlapped. Several studies have investigated the risk effects in a multi-predator context, revealing that multiple predators may create areas of contrasting risk or double-risk zones within the same landscape [13,67]. For example, Lone et al. (2017) [13] found that roe deer exposed to hunters and lynx faced overlapping yet contrasting landscapes of fear, showing that the presence of one predator can influence prey exposure to another. This aligns with our findings that hunting risk interacts with areas of high wolf density, leading roe deer to dynamically adjust their habitat selection. Wild boar drive hunting induces high-intensity human disturbance, with many hunters and dogs, which likely amplifies risk perception and causes roe deer to alter their habitat selection more strongly during this time. These findings align with Norum et al. (2015) [67], who demonstrated that roe deer responses to human hunting strategies varied significantly, with notable differences between drive hunting and sit-and-wait hunting. When the hunting season ends, roe deer no longer select areas with high wolf density, which strongly underlines that this effect is driven by human activity, indicating how hunting can profoundly shape predator–prey relationships, as demonstrated in other studies [68].

To conclude, our findings emphasize the importance of considering both human-induced and natural predation risks in shaping prey spatial behavior, especially in multi-use landscapes where protected areas are interspersed with zones of active human hunting. These results underscore the importance of considering anthropogenic influences when analyzing predator–prey spatial dynamics, in order to find solutions to improve human–wildlife coexistence while engaging all different stakeholders in the process [69]. Given the temporal and spatial heterogeneity in roe deer responses, a one-size-fits-all approach to hunting regulations and tourism management may not be effective. Spatially explicit management strategies, such as zoning hunting activities to separate human disturbance areas from key wildlife habitats, could help balance human use and conservation goals [70]. While protected areas play a critical role in reducing direct human impacts, stronger efforts are needed to manage human activities within these areas, particularly in mitigating the perceived risks associated with recreational activities. Ensuring sufficient habitat connectivity of refuge options can help ungulates navigate complex landscapes of fear. In the Anthropocene era, human disturbance can even exceed the spatial effects of risk induced by apex predators [68,71]. In habitats becoming progressively more human-dominated, understanding the impact of human activities on wildlife behavior will become increasingly important for effective conservation and management strategies to develop human–wildlife coexistence.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17020115/s1, Table S1: List of covariates included in the fitted models as explanatory variables. https://data.mendeley.com/drafts/dfbpd4h9bj (accessed on 31 January 2025) [72].

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Data Availability Statement: The data presented in this study are available on request from the corresponding author upon reasonable request.

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The Status and Spatial Patterns of Poaching, Illegal Trade, and Human–Bear Conflict of Asiatic Black Bears in China, 2010–2020

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Abstract: Asiatic black bears (*Ursus thibetanus*) are a large carnivore, widely distributed in East, South, and Southeast Asia. However, they have experienced dramatic population decline across this range due to various anthropogenic threats. The great demand for bear parts in the black market exposes this species to intense pressure of being poached and then illegally traded. Meanwhile, the continuous expansion of anthropogenic land use results in the sharpening of human–bear conflicts. In this study, we conducted a comprehensive search and collected information of the poaching, illegal trade, and human–bear conflict events related to Asiatic black bears reported in China during 2010–2020. By systematically searching judicial adjudicative documents and news reports, we identified 351 (64 poaching, 221 illegal trade, and 90 conflict) events across the country. The results showed that Southwest China was a hotspot across all categories (41, 149 and 40 events, respectively). Bear paws were the most common type of bear parts found in illegal trade (52.1%), and the most frequently reported human–bear conflict form was human injury from bear attacks (at least 52 people injured and another 7 killed). By determining the status of black bears being poached, traded, and their conflicts with humans in China, these results will provide important insights into the further research and conservation of this iconic species.

Keywords: wildlife trade; poaching; human–wildlife conflict; human–bear conflict; *Ursus thibetanus*

1. Introduction

Asiatic black bears (*Ursus thibetanus*) are a large ursid species, mainly distributed in East, South, and Southeast Asia [1,2]. As an omnivorous large mammal with a broad dietary spectrum, Asiatic black bears are adaptable to various forested habitats, including boreal coniferous forests, temperate deciduous forests, subtropical evergreen forests, and tropical rain forests [1–3]. They play important roles in the ecosystems they inhabit, with critical ecological functions such as seed dispersal and carcass scavenging [2,4,5]. They are also considered an effective umbrella species, since they have good coverage of the ecological needs of numerous sympatric species and the ability to be more persistent to environmental disturbances than other large carnivores [6].

Across their distribution range, Asiatic black bears have been facing severe threats of habitat loss and direct killing from humans, resulting in dramatic population decline and range shrinkage over the past century [1,2,7,8]. Traditionally, Asiatic black bears are widely hunted for their fur, meat, and various body parts with specific uses. For example, bear gallbladder and fat have been long used as traditional medicine in Asian countries, and

bear paws are considered a rare food with high nutrition [9,10]. Although the species is now listed as vulnerable in the IUCN Red List of Threatened Species [1], listed in Appendix I of CITES and listed as protected wildlife in many countries, the huge demand for black bear parts and derivatives in the black market has imposed substantial poaching pressure on its wild populations [11–13]. Bear parts and even live bears, primarily young cubs who will be raised as bile producers in bear farms and play animals in circuses, are popular goods in illegal wildlife trade [7,14–17]. Poaching and related illegal trade are believed to be one major direct threat to this species [1,2].

Meanwhile, with the rapid increase in the human population and expansion of anthropogenic land use, conflicts between wildlife and humans have become sharpened [18–20]. Asiatic black bears are also frequently involved in human–wildlife conflicts, i.e., human–bear conflicts. These conflicts often include crop damage (as well as damage to various types of plantations) [21–23], beehive damage [19], depredation of livestock [21,24,25], and human injury from Asiatic black bears [26,27]. If these human–bear interactions cannot be managed well and losses to local residents during these conflicts are not compensated, these conflicts will be further intensified, leading to retaliatory killing of bears [21,28] and imposing additional pressures to this vulnerable species.

Among the 17 countries that still have wild populations of Asiatic black bears, China is considered the one with the largest wild population and the largest area of suitable habitats [1,20,29]. However, Asiatic black bears have been eliminated from many regions within the country, especially in Northeast, North, Central, and South China [1,8,29,30]. Previous studies indicate that there are currently six regional populations in Mainland China and two island populations (i.e., Taiwan and Hainan) [30]. However, their habitats are highly fragmented, especially in East and South China, and the population of Hainan Island may have vanished [30]. Asiatic black bears are listed as Class II national protected animals in China [31], but poaching and retaliatory killings following human–bear conflicts are still believed to be major threats to this species [1,2]. These isolated small populations are specifically vulnerable to illegal killings, since random loss of even a small number of individuals may drive the local population to extinction [32].

With the rapid growth of the Chinese economy over the past three decades, the demands for bear parts and derivatives in illegal markets are also increasing. Consequently, in addition to increased poaching pressure within China, a remarkable increase in transboundary wildlife trade has been reported, with bear parts illegally imported into China, mainly from Southeast Asian countries and Russia [12,16,33]. Though previous studies are mainly from Southeast Asian countries like Laos, Vietnam, and Myanmar, limited clues have indicated that China may play a considerable part in the illegal trade chain across various countries [16,34–36]. Asiatic black bears are also a common species involved in human–wildlife conflicts, but relevant studies are limited and mainly concentrated on Southwest China [19,23,28]. Therefore, determining the status, forms, and spatial patterns of these poaching, trade, and conflict events across the country has become an urgent task for wildlife researchers and managers. This will provide the critical knowledge needed to better understand the underlying drivers towards effective conservation of this threatened species.

In this study, by systematically searching judicial adjudicative documents (JAD) and news reports (news), we conducted a comprehensive review and collected information regarding poaching, illegal trade, and human–bear conflict events related to Asiatic black bears in China from 2010 to 2020. For the identified events, we extracted specific information like the date, location, number of bears involved, etc., and we used this information to address the following questions: (1) What are the spatial patterns of the three categories of events? (2) Are the number of poaching and human–bear conflict events correlated with the area of suitable habitat? (3) What is the frequency of different types of bear parts found

in illegal trade? (4) What are the forms of reported human–bear conflicts? Through this study, we hope to fill our knowledge gap regarding the status of Asiatic black bears being poached, traded, and their conflicts with humans in China. The information and results may serve as a baseline and will provide valuable insights into the conservation of this species in the future.

2. Materials and Methods

2.1. Data Collection

During June of 2021 and December of 2023, we conducted a comprehensive review on the poaching, illegal trade, and human–bear conflict events related to Asiatic black bears in China during 2010–2020 by systematically searching JAD and the news. The data resources of this study include: (1) JAD: Using the advanced search function of the "China Judgements Online" dataset (https://wenshu.court.gov.cn/, accessed on 10 December 2023), we searched for relevant cases of poaching and illegal trade of black bears with words in panel A and combined them with each cause of action shown in panel B of Table 1. We also searched for cases of human–bear conflict with "black bear" as the full-text search keyword and "administrative assistance" as the type of action. (2) News: We searched in the two most popular searching engines in China, i.e., Baidu (https://www.baidu.com/, accessed on 5 June 2021) and Google (http://www.google.cn/, accessed on 12 August 2021), using the combinations of keywords in panels A and B of Table 1, and the time limit was constrained from 1 January 2010 to 31 December 2020. We checked all the results returned and then identified the records of our target events. Given that these two engines may have poor coverage in Taiwan, we also searched the news website China Times (https://www.chinatimes.com/?chdtv, accessed on 20 October 2021) of Taiwan using the terms "black bear" and "moon bear" (another commonly used name for black bears in Taiwan) as the keywords for supplementary information of related events on this island. Among all the raw records generated from the news report search (approximately 3000 records), we first removed all duplicates that were forwarded from the same initial source, then we excluded the ones solely from single sources without direct evidence (e.g., photographs or videos) and only retained the ones from multiple ($\geq$2) sources or with direct evidence. All the news records retained for subsequent analysis were from reputable news media and government agencies such as forestry police departments.

Table 1. Keywords used in JAD search and news search in search engines.

	JAD	News
A [1]	[full-text search keyword] black bear [3] [type of action] criminal cases	China black bear
B [2]	[cause of action] illegally hunt and kill rare and endangered wild animals which are under the state key protection	poaching/poach hunting/hunt
	[cause of action] illegally purchase, transport or sell those rare and endangered wild animals and their manufactured products	trading/trade hurting people
	[cause of action] violate hunting law and regulations	beehive/bee farm human-bear conflict

[1] All words in this panel were used for the search. [2] Every time, each word in this panel was used combined with the words in panel A. [3] Contents in square brackets represent different search bars.

2.2. Data Processing

We recorded the unique case number of each judicial adjudicative document and the site URL of each news report. If there were multiple documents or reports for the same event, we kept the one with the most complete information and considered the others as duplicates, which were excluded from the analysis.

We sorted all records into three categories according to the type of event: poaching, illegal trade, and human–bear conflict. We collected the specific information of each event of the three categories (Table 2). We classified the type of bear parts and derivates reported in illegal trade events as follows: paw, head, gall bladder and derivates, meat, claw and tooth, whole body, live animal, fur, fat, bone, and genital. Because multiple types of bear parts could be involved in one event, and some types of bear parts were uncountable (e.g., meat, fat), we calculated how many times each type of bear part appeared through all events instead of the number of specific bear parts.

Table 2. Specific information recorded for poaching, illegal trade, and human–bear conflict events.

Poaching	Illegal Trade	Human–Bear Conflict
time of poaching	time of trading	time of conflict
site of poaching	site of trading	site of conflict
poaching method	agency conducting the seizure	form of conflict
number of bears poached	type of bear products confiscated	number of human injuries and/or deaths
treatment of bears poached	number of bears confiscated [1]	number of livestock/poultry lost
agency conducting the seizure	number of live bears seized [2]	number of bears causing trouble
whereabouts of live bears seized	whereabouts of live bears seized	state of bears causing trouble
		whereabouts of the bears after the conflict

[1] Sometimes inferred from the number of bear parts. [2] For cases where live bears, primarily young cubs, are sold.

Conflict events were divided into six forms: human injury/death, beehives damage, property damage, intending to enter/entering human living region, livestock/poultry depredation, and crop damage. Here, we referred to residential areas, schools, and farmland as "human living regions", and we combined damages of fruits and other plantations from black bears into "crop raiding". Since more than one form of conflict can happen during one event, we viewed each form in every single event as one incident, then we counted how many times each form appeared through all incidents rather than through all events.

For all the identified events, we extracted the geographic location of each site. We queried the center coordinates (longitude and latitude) of the smallest land unit (e.g., villages, protected areas, parks, timberlands, etc.) using Google Earth (https://www.google.com/maps/, accessed on 20 December 2023) or Baidu Maps (https://map.baidu.com/, accessed on 20 December 2023). We then created a vector point layer for each category of events (see the online shared dataset of this article) in ArcGIS 10.5 (ESRI Inc., Redlands CA, USA) for subsequent analysis.

2.3. Data Analysis

We examined whether there was a correlation between the number of the three categories of events, respectively, and the area of suitable habitat in each provincial administrative region (hereafter referred as province. See province names in Figure S1).

We used the fine-scale distribution map of Asiatic black bears (binary raster, raster resolution 3 km × 3 km) produced by Shen et al. [30] to calculate the suitable habitat area in each province (presented as number of grid cells) using ArcGIS 10.5. We then conducted a regression analysis in R 4.2.2 [37] to examine the correlation between the number of events and the habitat area. Those provinces with 0 records were excluded from this analysis.

3. Results

We collected 351 records (241 from JAD and the remaining 110 from news) and identified 375 events in total (24 records contained both poaching and illegal trade events), including 64 poaching, 221 illegal trade, and 90 human–bear conflict events (Figure 1).

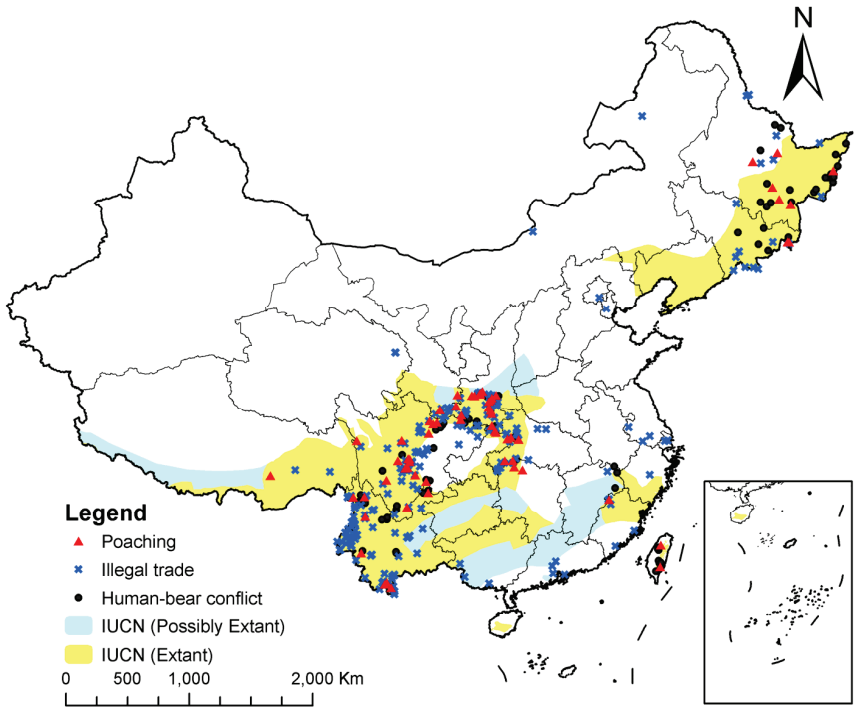

Figure 1. The spatial distribution of poaching, illegal trade, and human–black bear conflict of Asiatic black bears in China during 2010–2020. The species range map of Asiatic black bears from the IUCN Red List is displayed as the background.

3.1. Spatial Distribution

The poaching events (Figure 2a) were mainly reported in Southwest China, with some additional cases in Northeast China and East China. The mountainous areas around the Sichuan Basin, Northeast China, and the border regions in Western and Southern Yunnan Province were the three hotspots of reported poaching events. Eight poaching events happened in national nature reserves. The methods that bear poachers used included setting foot snares or traps, poisoning using baits with toxic chemicals, setting high-voltage electrical wires, using bait mounted with hand-made explosives, and directly shooting with guns.



Figure 2. The number of poaching (**a**), illegal trade (**b**), and human–bear conflict (**c**) events reported in each province of China during 2010–2020.

The illegal trade events (Figure 2b) showed a spatially clumped pattern that could be grouped as three types: (1) at the surrounding mountainous areas of Sichuan Basin, which also overlapped with the largest hotspot of poaching events; (2) at the border regions between China and Southeast Asian countries (i.e., Myanmar, Laos, and Vietnam) and Northeast Asian countries (i.e., Russia and North Korea); and (3) in the areas around big cities in the eastern part of China (e.g., Shanghai and the Guangzhou–Shenzhen–Hongkong urban agglomeration) (Figure 1).

The human–bear conflict events (Figure 2c) mainly concentrated in both Northeast and Southwest China, with sporadic occurrences in Central China. Taiwan of East China was also a hotspot for human–bear conflict.

There were 60 out of 64 poaching events located within the IUCN range map, with 84.4% (n = 54) in the Extant category and 9.4% (n = 6) in the Possibly Extant category (Figure 1). Among the 90 human–bear conflict events, 82.2% (n = 74) were in the Extant category and 1.1% (n = 1) were in the Possibly Extant category, whereas 16.7% (n = 15) fell outside of the range map (Figure 1). At the province level, nine provinces that are included in the IUCN range map with an Extant distribution were found with neither poaching nor human–bear conflict events.

The relationship between the number of human–bear conflict events with area of suitable habitat at the province level are shown in Figure 3. We found no correlation between either the number of poaching events or the number of illegal trade events and habitat area, whereas the number of conflict events was positively correlated with suitable habitat area (a = 0.002, b = 2.98, R^2 = 0.69, $p < 0.05$).

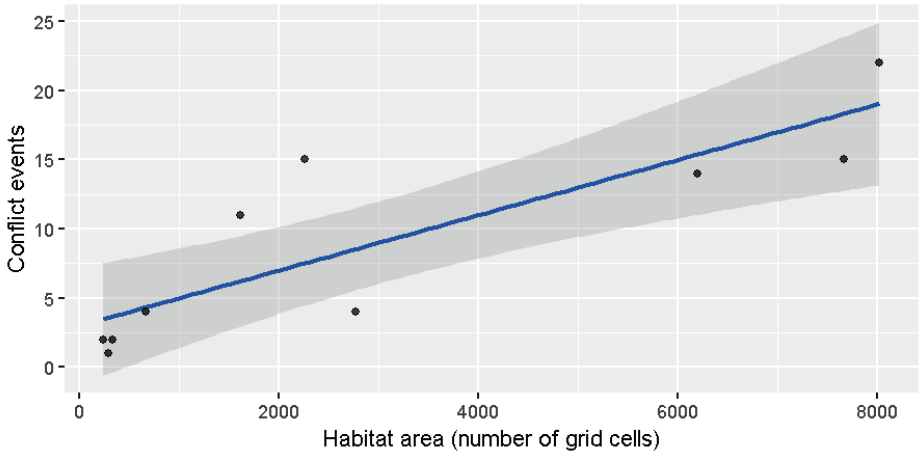

Figure 3. The relationship between the number of human–bear conflict events and suitable habitat area at the province level in China. The solid blue line indicates the median predicted line, and the shaded areas show the 95% confidence interval.

3.2. Bear Parts in Illegal Trade

For 213 out of the total 221 illegal trade events, we found that bear paws were the most frequently traded type (reported in 52.1% of all the 213 illegal trade events), followed by bear meat (18.3%) and whole body (15.0%) (Figure 4). Among all illegal trade events, there were 43 live bears involved. In the remaining eight events, the types of bear parts and derivates were unknown.

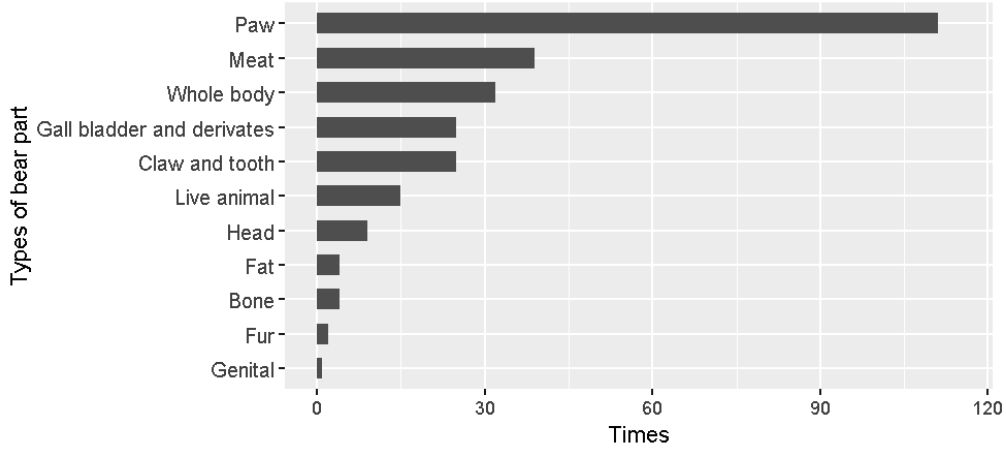

Figure 4. Frequencies of different bear parts appearing in illegal trade events (n = 213) in China, 2010–2020.

3.3. Forms of Human–Bear Conflict

As shown in Figure 5, the most frequently reported form of human–bear conflict was human injury/death (55.3%), followed by beehives damage (18.1%) and intending to enter/entering human living region (10.6%). At least 52 people were injured and another 7 were killed in the cases where severe conflicts occurred during unanticipated encounters.

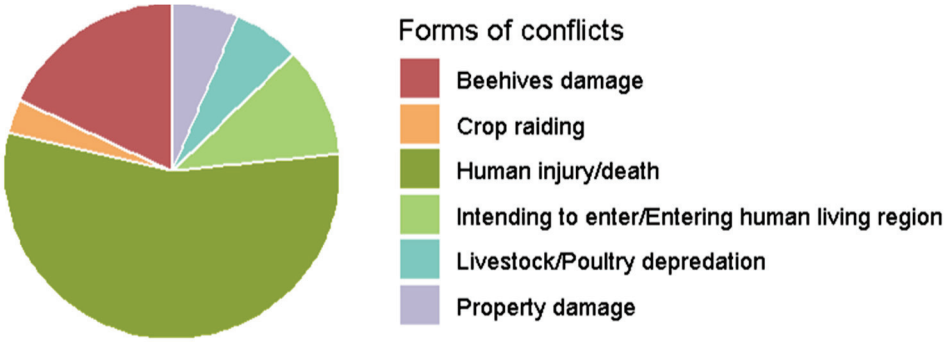

Figure 5. Proportion of different forms of conflict reported in human–bear conflict events in China, 2010–2020.

4. Discussion

4.1. Poaching

Intuitively, poaching of black bears and human–bear conflict involve mainly direct encounters between humans and bears; therefore, areas with more bears would have a higher probability of these two categories of event occurring. But, our regression results showed that only conflict events were significantly related to habitat area, whereas poaching was not. This might be due to two possible reasons that were not considered in this analysis due to lack of information:

(1) Human motivations behind poaching are complicated and could be influenced by various drivers. In general, higher market demands for black bear parts will lead to higher poaching motivations [11] (pp. 1–2). Apart from personal use or economic benefits as common initial motives of poachers, some poaching events occur due to retaliation to "problematic bears" by local residents following their crop or livestock loss and the intention to prevent further damage [21,22,28]. We also found in some poaching events black bears were not the intended target but were captured in traps set for other animals like boars or small ungulates, which has also been reported in other areas [38,39].

(2) The intensity of poaching is also related to the efficiency of local protection and law enforcement, which is however difficult to quantitatively measure. Protected areas, especially nature reserves in the case of China, are the backbone in protecting threatened wildlife from illegal harvest [40]. From the 1990s, the total number and area of nature reserves in China have increased rapidly [41], and patrols in reserves have proven an effective approach in reducing the poaching of wildlife [28]. However, the management strength may vary broadly among reserves, leading to highly varied conservation effectiveness [42]. Meanwhile, many bears and habitats are not yet covered by reserves, and some reserves are not big enough to comprise the home range of Asiatic black bears [43]. Therefore, the ability to protect black bears differs across reserves and regions, and as a result, the occurrence of poaching event varies among provinces. These issues will all influence the intensity of bear poaching.

4.2. Illegal Trade

Given that the illegal trade events do not involve direct interactions between humans and Asiatic black bears, they may not necessarily occur in the bear habitat or at the site where the bear was captured or poached. It was not a surprise that we found no correlation between the number of illegal trade events and habitat area.

In this study, we found that paws were most frequently traded, maybe because many people still hold the view that bear paws are high in nutrition. And, likely for the same reason, bear meat was the second most frequently traded type of bear part. Gall bladder only accounted for ~10% of bear parts illegally traded in China, which is very different from studies in other Asian countries where the gall bladder (and its derivatives) was the most common and frequently traded bear part (e.g., in Lao PDR [33] and India [44]). The potential reason may be partly because bear bile products from licensed bear farms are legal in China [10], which to a certain extent may relieve the pressure from black market demands for bear bile. Even so, the logic of whether establishing bear farms will contribute to the protection of wild black bears is still being questioned, since the preference for wild bear bile due to its unsupported "better quality" still exists [45,46]. Therefore, there is still a need for the publicity of alternatives of bear bile like synthetic bear bile. And, for other traded bear parts, the whole body and fur may be used as trophies and ornaments; claws and teeth are used as charms and ornaments [33,36]; live bears could be sent to bear farms or zoos [12,33]; and the rest may be traded for their purported medicinal properties [36].

Southwest China, especially Yunnan Province where China borders multiple Southeast Asian countries, is a hotspot for illegal trade events. In addition to the relatively high frequency of poaching by local residents, the wildlife trade across borders may also make a considerable contribution to black bear illegal trade [47]. In this study, we only included trade events in China and did not focus on international smuggling, which might underestimate the illegal trade in the country. This cross-border illegal trade could be considered from two perspectives:

(1) Bear parts and derivatives from abroad are sold in China. If we refer to a trade event as smuggling bear parts from foreigners at the border or parts that were seized at customs (entering China), then at least 22 events we recorded as international smuggling (sold into China), among which 16 events happened in Yunnan. Therefore, it is very possible that illegal trade with Southeast Asian countries (e.g., Myanmar, Vietnam and Lao PDR) accounts for the majority of bear parts smuggling in China.

(2) Bear parts and derivatives are sold from China to other countries. In addition to bear bile being exported to other countries in Southeast Asia (e.g., Singapore and Lao PDR) [11] (pp. 29–31, 38–40), there are also other types of bear parts like gall bladder [48] and even live bears [16] being illegally exported. Given that many border regions are remote areas with numerous trails hidden in the forests, bears or bear parts might be stealthily transferred across the border without being detected and captured by the authorities [12] (p. 19). Thus, in the future, the management agencies of China and neighboring countries should collaborate to strengthen law enforcement at the border regions with a high probability of bear distribution, like Northeast and Southwest China, to prevent the possible cross-border trade of bear parts and other wildlife.

4.3. Human–Bear Conflict

In this study, human injury/death was the most frequently reported form of human–bear conflict, followed by beehive damage. Livestock/poultry depredation and crop raiding only accounted for 6% and 3%, respectively. The major conflict form here is very different from that reported in previous studies, like crop damage [19,21,24,49] and

livestock depredation [25]. Additionally, the total number of conflict events is also much lower than other studies of human–black bear conflicts at a smaller scale, which mainly collected data through on-site interviews and questionnaires (e.g., Ali et al. [21] found 296 conflicts in Northern Pakistan). We believe that these differences are mainly due to the highly biased news transmitting phenomenon, where human injury/death receives much more attention than other conflict forms, so these cases were more reported in social media with high-level exposure. Most other conflict forms with minor impacts or financial losses, such as crop damage or livestock depredation, were therefore neglected and could not be found in the news. Such biases are also commonly seen in the human–wildlife conflicts involving other large carnivore species [50,51].

Among the 52 conflict events involving human injury or death, at least 46 happened in forests or mountainous areas, which coincides with the patterns reported in many previous studies that the majority of black bear attacks on humans happened in forests [21,24,28,52]. This could be explained by human expansion into bears' habitats [32]. Indeed, attacks on humans by large ursids are mainly caused by involuntary encounters and defensive action of females with cubs [53]. These events are also influenced by topography, vegetation, and their relatively limited eyesight; sometimes, black bears can only notice human presence within a very short distance, which may lead to shock and attack following involuntary encounters [19]. Meanwhile, black bear attacks were fatal in only five events in this study, which also supports the finding that attacks by ursids are much less fatal compared with other large carnivores (e.g., canids or felids) [53].

Bears may approach human residents for crop foraging or preying on livestock due to limited natural food in their natural habitats, especially before winter denning in years with poor mast production [54,55]. According to the Wildlife Protection Law and relevant policies in China, it is the wildlife management agency or local government who shall take the responsibility of compensating for the losses and damages caused by wildlife [56–58]. However, in practice, it is difficult for local residents involved in these conflicts to obtain this compensation. This may be due to various reasons, such as local people not being aware of or familiar with compensation policies [59], or it is difficult for the authorities to verify or quantify the loss claimed by local residents [59,60].

4.4. Conservation Implications

Based on the results of our study, we would like to provide some suggestions for future conservation of Asiatic black bears in China:

(1) Strengthen law enforcement and increase penalties for wildlife crimes, especially in Southwest China. Although in China, Asiatic black bears are listed as Class II national protected animals and trading or killing protected wildlife is prohibited by Criminal Law and Wildlife Protection Law, it is still possible to commit these crimes without being prosecuted and convicted [61]. Southwest China is a hotspot for both poaching and illegal trade events, which could be explained by the weaker enforcement in this remote and vast mountainous area. Thus, strengthening law enforcement in this region could intensify the law's deterrent effects and reduce these crimes [62].

(2) Raise the legal awareness of rural residents in Southwest China. Previous studies have shown that a large fraction of poacher who poach protected animals have an education level lower than senior primary school [63]. Therefore, some local villagers may not be fully aware of the seriousness of committing such crimes, and raising their legal awareness will prevent them being involved in poaching activities.

(3) Increase investment in wildlife protection. Although by 2020, China had achieved Aichi target 11 with a protected area coverage of more than 17% [64], increasing protected areas does not naturally guarantee their effectiveness in wildlife protection.

In China, the salary of reserve rangers may be much lower than the average wage [65], which may affect the eagerness and effectiveness of law enforcement. Meanwhile, a lack of funding would result in a shortage of necessary equipment and logistics needed for law enforcement [66], which also leads to an inability to detect wildlife crime.

(4) Enhance cooperation between neighboring countries to inhibit international smuggling of bear parts and derivatives. Clustering of illegal trade events at the border of Southwest China indicates active illegal trades between China and neighboring Southeast Asian countries, as reported in many previous studies (e.g., [16]). Cooperation between different countries should destruct the illegal trade chain from both ends.

(5) Improve the compensation mechanisms for wildlife damage. Asiatic black bears are a large carnivore that may cause great economic loss (e.g., from crop and beehive damage) to local communities, and they may become the primary species involved in human–wildlife conflict in some regions [67,68]. Consequently, black bears also face severe threats of retaliatory killing. Successful and timely compensation is considered an effective measure to avoid retaliatory killing of animals involved in human–wildlife conflicts [69]. In addition to government-leading compensation, commercial insurance specifically targeting crop/livestock loss owing to wildlife foraging/predation has been emerging as a promising approach to resolve human–wildlife conflict issues [70]. Wildlife managers and management agencies may consider integrating these new commercial approaches with traditional administrative policies to fulfil the needs of relieving the pressures on black bears from human–bear conflicts.

4.5. Potential Limits

Our study demonstrated that, compared with conventional interviews or questionnaire surveys, this keyword-searching method from JAD and news can collect highly reliable data on the poaching, illegal trade, and human–wildlife conflict of specific threatened species across a wide range.

However, researchers must be aware of the limits and potential bias of this method and the information collected. The records extracted from JAD and news may underestimate the target events that happened in the real world. The potential reasons include:

(1) Numerous poaching and illegal trade cases may not be discovered by the police and authority yet [71,72].

(2) The judgments of some seized cases may have not been pronounced or not been input to the online database yet. We can only collect JAD data after July 2013 from "China Judgement Online", which was launched at this time.

(3) Many human–wildlife conflicts with minor impacts (e.g., crop damages) do not receive significant attention from public media. For example, we found fewer events for a specific site or region compared to some onsite studies with extensive interview efforts: Liu et al. [28] reported at least 117 poaching events of black bears in Sichuan Province during 2003–2007, and Ji et al. [19] found 207 human–bear conflict events in Gaoligongshan National Nature Reserve, Yunnan Province during 2015–2019.

Nevertheless, this method still can serve as an effective approach to conduct quick scans to reveal the general large-scale patterns across the country, which is critical for national assessments and the development of effective conservation policies and action plans in a timely manner.

4.6. Other Implications and Conclusions

Among the three categories of events we collected, both poaching and conflict events could be considered as confirmed occurrence records of Asiatic black bears in China. Based

on the IUCN range map, although most of the 64 poaching sites (84.4% in the *Extant* and 9.4% in the *Possibly Extant* categories) and 90 conflict sits (82.2% in the *Extant* and 1.1% in the *Possibly Extant* categories) were inside the range, there were a few records falling outside (one in Sichuan, one in Hunan, and two in Heilongjiang provinces). The IUCN species range map has been widely used in regional and global biodiversity assessments and large-scale macro-ecology research [73,74], whereas the accuracy of this dataset, which is primarily based on expert knowledge, is also frequently disputed [29]. Previous studies have demonstrated that, with occurrence sites collected from field surveys or observation, sometimes combined with modern approaches of species distribution modelling, the species' distribution and range map could be greatly improved [29,30,75]. These sites we identified outside the current IUCN range could be incorporated into future assessment of this species and therefore contribute to the verification and future updating of its range map.

Meanwhile, we also noticed that few poaching and conflict events were reported in East and South China during 2010–2020, and none in Hainan Island. A previous study by Shen et al. [30] indicates that suitable habitats of Asiatic black bears in both East and South China are highly fragmented, and the bear populations in both regions are considered under high risk with the highest conservation priority level. Shen et al. [30] also speculated that this species may already be extinct in Hainan, since no confirmed record has been reported during the past decades despite substantial survey efforts on this large island. Our results further support the conclusions of Shen et al. [30] and suggest that systematic surveys, assessments, and conservation actions are urgently needed for the bears inhabiting East and South China.

In conclusion, through collecting and organizing relevant information regarding poaching and illegal trade of Asiatic black bears and their conflicts with human reported in China during 2010–2020, we revealed the common patterns of these three categories of events across the country. Our results showed that Southwest China was the hotspot of all three categories of events. Bear paws were the most common type of bear parts found in illegal trade (52.1%), and human injury/death from bear attack was the most frequently reported form of human–bear conflict. We suggest that the authorities strengthen law enforcement and raise legal awareness in Southwest China, especially increasing investment in wildlife protection, enhancing international cooperation to reduce smuggling, and improving compensation mechanisms to alter people's negative attitudes towards black bears.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17020093/s1.

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Conservation Strategies for Xishuangbanna: Assessing Habitat Quality Using the InVEST Model and Human–Elephant Conflict Risk with Geographic Information System

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Abstract: Xishuangbanna, located in southern Yunnan, China, is a vital tropical rainforest reserve supporting rich biodiversity, including the endangered Asian elephant (*Elephas maximus*). Increasing human activities, such as urbanization and agricultural expansion, have degraded habitats and intensified human–elephant conflicts, adding to the challenges of conservation. This study integrates habitat quality assessment and conflict risk analysis using the InVEST model across 2128 villages, considering land use and habitat threats like cropland and roads. The model reveals significant overlap between high-conflict zones and low-quality habitats near key reserves, underscoring the need for targeted conservation strategies. We propose establishing Ecological Source Areas (ESAs) to protect high-quality habitats and Ecological Restoration Zones (ERZs) to improve ecological conditions in low-quality, high-conflict zones. ESAs are essential for providing continuous ecosystem services and ensuring ecological security, while ERZs focus resources on areas with high conflict risk that urgently need restoration. Additionally, we recommend creating ecological corridors to connect fragmented habitats, enhance connectivity, support herd interactions, and reduce conflicts by expanding elephants' safe roaming range. This integrated framework emphasizes habitat protection, ecological restoration, and conflict mitigation while accounting for human dynamics to support sustainable conservation. Reducing overlap between human and elephant activities remains a key objective. Future research should refine these models with more detailed data and extend their application to other regions, focusing on adaptive management and monitoring to address evolving ecological and human dynamics.

Keywords: Xishuangbanna; Asian elephant; human–elephant conflict; habitat quality; InVEST model; conservation planning

1. Introduction

The Asian elephant (*Elephas maximus*), a keystone species vital to the ecological balance of Asian tropical forests, faces increasing threats from habitat fragmentation and human–elephant conflicts, particularly in the Xishuangbanna region of southern Yunnan, China [1,2]. Since 1976, the Asian elephant population in Xishuangbanna has fluctuated

(Table 1), impacted significantly by human activities, including extensive deforestation for rubber plantation development [3–5]. Recent enhanced conservation measures have brought the population to about double what it was in 2005–2006 [6]. However, the species remains critically endangered. Habitat degradation and expanding human activity are leading to increases in both the frequency and severity of conflicts [7–9]. This habitat degradation and increased conflict put the recent elephant population gains and sustainable practices at risk, underscoring the urgent need for effective conservation strategies that address both ecological and social dimensions [10,11]. There is not currently a target elephant population value for Xishuangbanna. This is a gap that needs to be addressed soon to further guide conservation measures and protect against human–elephant conflict.

Table 1. Estimated Asian elephant populations in Xishuangbanna from 1976 to 2014.

Year	Population (Approx.)
1976	101
1983	213
1997	165 to 197
2003	187 to 217
2005–2006	132 to 149
2014	228 to 279

Habitat quality is a fundamental determinant of an ecosystem's capacity to support wildlife and maintain biodiversity [11,12]. Understanding how habitat quality is influenced by various disturbances, both natural and anthropogenic, is important in planning and prioritizing conservation strategies. Disturbances, whether natural or anthropogenic, play a critical role in shaping ecosystems. Disturbances such as urbanization, agricultural expansion, and infrastructure development can degrade habitats and fragment ecosystems [13]. Moderate disturbances can sometimes enhance biodiversity and species coexistence by creating habitat mosaics and promoting ecological succession. However, excessive or frequent disturbances often result in irreversible degradation [14].

In Xishuangbanna, rapid urbanization, agricultural expansion, and infrastructure development have significantly transformed land use and land cover, resulting in habitat loss and degradation [15]. Although substantial research has been conducted on habitat fragmentation and human–wildlife conflicts, integrated assessments evaluating both habitat quality and conflict risks are urgently needed in regions experiencing these rapid environmental changes [16,17]. Innovative approaches combining spatial analysis, ecological modeling, and conflict data provide avenues for developing targeted conservation strategies that address both ecological and human dimensions [18].

There are currently many methods for evaluating habitat quality, but it is essential to consider the influence of ecological disturbances in this process. Drawing on the theoretical framework of disturbance ecology, this study integrates multiple threat factors, such as cropland, roads, and villages, to assess their spatial impacts on habitat quality. These insights align with the work of Salafsky et al. and Wohlgemuth et al., highlighting the dynamic role of disturbances in shaping ecosystem resilience and biodiversity [13,14].

One commonly used method is conducting field surveys to construct habitat quality assessment indicators. This method requires a large amount of human and material resources and is time-consuming and labor-intensive. As such, it is only suitable for small-scale research. It is too difficult to use in large-scale habitat quality assessments [19]. Another commonly used method is to use models to evaluate habitat quality. This method involves using various modern technological means, such as remote sensing technology and GIS technology, to establish mathematical models to evaluate habitat quality [20,21]. The advantage of this method is that it can quickly obtain large-scale habitat ecosystem quality information and can be evaluated at different scales according to needs. Among these habitat quality models, the widely used InVEST model has the advantages of easy parameter acquisition, the visualization of results, etc. [22,23]. Moran's I spatial autocorre-

lation analysis is used to identify clusters of high and low habitat quality, providing spatial pattern insights to further guide priority conservation [24].

In addition, a GIS-based human–elephant conflict risk model was developed as part of this study using insurance claim data to simulate the human–elephant conflict risk level of the entire study area. The claim data included the location and extent of damage, making it a good method for measuring conflict risk and impact. This integrated approach can identify high-risk areas and provide a detailed understanding of the dynamics of conflict space, which is crucial for developing targeted conservation strategies.

Through the innovative integration of NDVI, GIS, and the InVEST model, this study's aim is to improve the accuracy of habitat quality evaluation, providing valuable guidance for regional conservation planning. These findings have broader implications for similar conservation challenges worldwide, emphasizing the need for multifaceted approaches to protect wildlife in rapidly changing landscapes.

This is not a study of the elephants themselves; it is a study of the elephant's habitat and of human–elephant conflict risks. The primary goal of this study is to assess habitat quality and human–elephant conflict risk for Asian elephants in order to develop effective conservation strategies that support the long-term survival of the species. While calculating human–elephant conflict risk, we focused on incident data, specifically insurance claims data, as these directly reflect human–elephant conflict occurrences. However, in constructing the model, we also included relevant variables such as cropland distribution, open woodland areas adjacent to cropland, and slope. These factors have been validated by previous studies as key areas where human–elephant conflicts are likely to occur [25]. Additionally, when assessing habitat quality for Asian elephants, we carefully considered habitat suitability specific to this species. Parameter selection was guided by published research on Asian elephant habitats in Xishuangbanna, incorporating primary threat factors such as cropland, village roads, settlements, and orchards to evaluate habitat quality [26,27]. This ensures that the model accounts for environmental factors directly relevant to Asian elephants and their habitat needs, rather than solely focusing on conflict-related variables.

2. Study Area

The Xishuangbanna Dai Autonomous Prefecture in the southern part of Yunnan, China, is situated in the Hengduan Mountains (Figure 1). The geographic coordinates range from 21°08′ to 22°36′ N latitude and 99°56′ to 101°50′ E longitude, encompassing an area of approximately 19,100 km^2. The topography of Xishuangbanna is characterized by high elevations surrounding a lower central basin, creating significant terrain variations across the region [28].

The region experiences a tropical monsoon climate with an average annual temperature exceeding 20 °C and annual precipitation reaching 2491 mm. These humid climatic conditions are conducive to the growth of tropical rainforests. However, the rapid increase in human population and the expansion of economic crops such as rubber, coffee, and tea have substantially altered land use patterns, which in turn has led to the significant fragmentation of the elephants' original habitat areas [29].

The intensification of human activities, particularly agricultural expansion and infrastructure development, has directly impacted the range and distribution of the Asian elephant, exacerbating human–elephant conflicts in the region. In response to these ecological challenges, the Yunnan Xishuangbanna National Nature Reserve was established in 1958 to protect this critical ecosystem [30]. The reserve spans Menghai County, Jinghong City, and Mengla County, comprising five geographically distinct sub-reserves: Mangao, Mengla, Menglun, Mengyang, and Shangyong. These sub-reserves encompass extensive areas of tropical rainforests and host the largest and most concentrated populations of Asian elephants. Despite these conservation efforts, ongoing human encroachment and land use changes continue to pose significant threats to habitat integrity and have intensified human–elephant conflicts within and around the reserve [31].

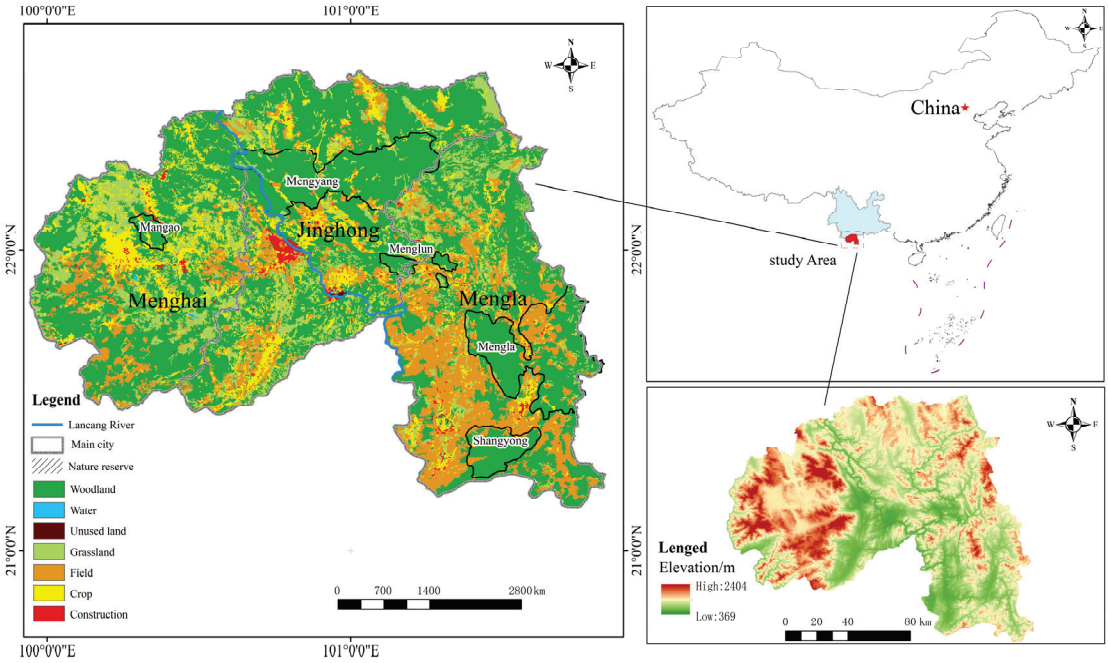

Figure 1. Location, terrain types, geopolitical boundaries, and elevations of the study area.

3. Data Sources and Research Methods

3.1. Data Sources

This study utilizes a diverse range of data sources, as detailed below. All raster data were processed using ArcGIS 10.8, projected uniformly to the WGS_1984_UTM_Zone_48N coordinate system and reclassified into a 1 km × 1 km grid format to ensure data consistency and comparability.

Land Use Data: The land use data for the study area for the year 2020 were sourced from the Resource and Environment Science and Data Center, Chinese Academy of Sciences (https://www.resdc.cn, accessed 27 February 2023), with a resolution of 1 km × 1 km.

Normalized Difference Vegetation Index (NDVI) Data: NDVI data were sourced from the Earthdata platform (https://earthdata.nasa.gov, accessed 16 April 2023) and used to assess habitat quality.

Road Network Data: Road network information was derived from OpenStreetMap (OSM) (https://www.openstreetmap.org, accessed 4 July 2023), covering all roads within the study area.

Socioeconomic Data: The socioeconomic data of 2128 natural villages were sourced from the Yunnan Digital Rural Network (http://www.ynszxc.gov.cn, accessed 6 May 2018), including information on population and economic activities. Natural villages are settlements that form organically over a long period, with residents living close together within a specific natural environment. Typically, villagers share the same surname and lineage, descending from a common ancestor. Village point data were sourced from the National Catalogue of Geographical Information Resources (https://www.webmap.cn, accessed 10 May 2023). Administrative village boundaries were sourced from the National Geographic Information Public Service Platform, Tianditu (http://www.tianditu.gov.cn, accessed 10 May 2023). Administrative villages are the lowest level of governmental body and often comprise multiple natural villages.

Human–Elephant Conflict Compensation Data: Data on compensation for damages caused by human–elephant conflicts were provided by the Xishuangbanna Branch of China Pacific Property Insurance Co., Ltd., Xishuangbanna, China, and were used to analyze the impacts of such conflicts.

3.2. Research Methods

Habitat Quality Assessment Model

This study employed the Habitat Quality module of the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) model to evaluate habitat quality in the study area. The InVEST model integrates land use and land cover data, the spatial distribution of threat factors, their respective weights, and the maximum impact distances of threat factors to calculate habitat degradation [32]. The primary threat factors selected for the model were cropland, construction land, orchards, roads, and village development levels due to their significant impacts on habitat quality [26,27].

(1) Evaluation of Village Impact on Habitat Quality through Development Indicators

To evaluate the impact of villages on habitat quality, data were collected from 2128 villages in the study area using 28 development-related indicators across five indicator groups: resources, population, economy, infrastructure, and energy (Table 2). Indicators were standardized to ensure comparability and eliminate dimensional differences. The Entropy Weight Method was subsequently used to calculate the weight of each indicator.

Table 2. Hierarchical structure of indicators for evaluating economic development and its impact on habitat quality.

Indicator Group	Indicator	Indicator Code
Resource Indicators	Common cultivated land area	X11
	Paddy field area	X12
	Dry land area	X13
	Per capita cultivated land area	X14
	Forest area	X15
	Economic forest and orchard area	X16
	Per capital economic forest and orchard area	X17
Population Indicators	Rural population	X21
	Agricultural population	X22
	Labor force	X23
	Number of people engaged in primary industry	X24
	Population with college degree or above	X25
	Population with secondary education	X26
	Population with primary education	X27
Economic Indicators	Total rural economic income (per CNY 10,000 per year)	X31
	Income from cash (per CNY 10,000 per year)	X32
	Income from planting industry (per CNY 10,000 per year)	X33
	Income from animal husbandry (per CNY 10,000 per year)	X34
	Income from Secondary and Tertiary Industries (per CNY 10,000 per year)	X35
	Per capita net income of farmers (per CNY 1 per year)	X36
Infrastructure Indicators	Distance to nearest station (km)	X41
	Distance to nearest market (km)	X42
	Number of cars	X43
	Number of agricultural transport vehicles	X44
	Number of motorcycles	X45
	Number of tractors	X46
Energy Indicators	Number of households with biogas pools	X51
	Number of households with solar energy	X52

The specific steps performed are described below.

Data Normalization: The raw data were normalized to standardize all indicator values to a comparable range.

Entropy Calculation: The entropy value e_j for each indicator was calculated based on the normalized data: $e_j = -\frac{1}{lnm}\sum_{i=1}^{m} P_{ij} lnP_{ij}$, where P_{ij} represents the normalized value of village i for indicator j, and m = 2128 is the total number of villages.

Weight Calculation: Using the entropy values, the weight W_j of each indicator j was computed: $W_j = \frac{1-e_j}{\sum_{j=1}^{m}(1-e_j)}$, where m is the total number of indicators [33,34].

Indicator Standardization: Two different formulas were used to standardize the indicators. z_{ij} represents the standardized value for indicator j in village i. For positive indicators, the formula $z_{ij} = \frac{a_{ij}-min(a_{ij})}{max(a_{ij})-min(a_{ij})}$ was used. For negative indicators, the formula $z_{ij} = \frac{max(a_{ij})-a_{ij}}{max(a_{ij})-min(a_{ij})}$ was used. In both formulas for z_{ij}, $min(a_{ij})$ is the minimum value for a given indicator (j) across all villages, and $max(a_{ij})$ is the maximum value for a given indicator (j) across all villages.

Using these weights, the Technique for Order Preference by Similarity to an Ideal Solution (TOPSIS) was applied to calculate a comprehensive score for each village, determining their relative impact on habitat quality. A higher score indicates a greater negative impact on habitat quality. Each village was assigned to one of five village groups (Village I through Village V) based on this comprehensive score using the natural breaks classification method. The villages with the lowest comprehensive scores were assigned to Village I and the villages with the highest comprehensive scores were assigned to Village V.

(2) Determination of Maximum Impact Distances

Each threat factor, such as cropland or roads, impacts the habitat quality of the area around it. This impact is felt not only in the immediate vicinity of the threat, but also further way from the threat into the habitat area, though at diminishing magnitudes. A road has a very significant impact on habitat quality a few meters from its side. An impact on habitat quality is still felt 1 km away from the side of the road, though the magnitude of this impact is less. A threat factor's impact on habitat quality decreases either linearly or exponentially with respect to distance. The maximum impact distance of a threat is the distance at which the threat factor's impact reaches its first inflection point.

To accurately estimate the maximum impact distances of various threat factors, the Normalized Difference Vegetation Index (NDVI) was used as a proxy indicator for habitat quality [35]. ArcGIS distance analysis tools were applied to examine the trend of NDVI values in relation to increasing distances from the identified threat factors. The analysis revealed that the maximum impact distances for different threat factors varied between two and four kilometers (Figure 2) [36,37]. These calculated maximum impact distances were incorporated into the model to capture the spatial influence of each threat factor on habitat quality.

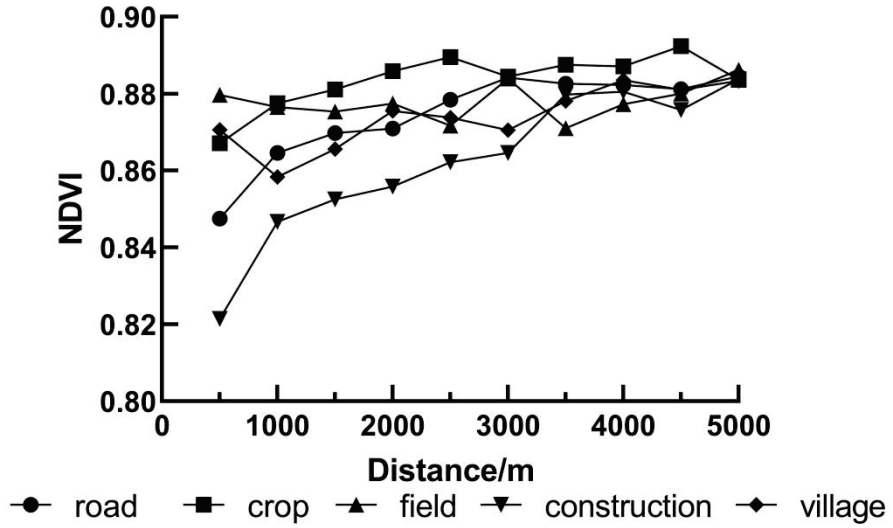

Figure 2. Assessment of impact distance of threat factors based on NDVI.

The data for this calculation were based on previous research on Xishuangbanna habitats conducted by our research group. To determine the maximum impact distance of threat factors, the NDVI values for the habitat types (forest land, sparse forest land, shrubland, grassland) were used. Using ArcGIS's nearest neighbor analysis tool in the distance analysis module, the shortest distance from each habitat point to a nearby threat factor was calculated. Then, in Excel, the average NDVI values were calculated at intervals of 500 m. These data were organized and summarized to create a trend graph showing how NDVI changes with increasing distance from threat factors. According to the trend graph, the maximum impact distance of a threat factor based on NDVI is determined by identifying the first inflection point where NDVI begins to level off after showing a rising trend with increased distance. Beyond this maximum impact distance, NDVI no longer increases significantly, indicating that the influence of the threat factor on vegetation cover in the habitat becomes negligible.

(3) Calculation of Habitat Degradation and Quality

Based on the analysis results, the weights and spatial decay types for each threat factor were determined (Table 3). These weights were determined by referring to published studies on Xishuangbanna habitats, from which an average weight was calculated [38,39]. The classification was tailored to the specific conditions of Xishuangbanna, with sensitivity parameters established for each threat factor based on local conditions and relevant literature (Table 4). The sensitivity of the threat factors was based on related published research on Xishuangbanna habitats [26,38–40].

Table 3. Maximum impact distance and weight of threat factors.

Threat Factors	Maximum Impact Distance (km)	Weight	Spatial Decay Type
Road	3	0.6	Linear
Crop	2.5	0.4	Exponential
Field	3	0.7	Exponential
Construction	4	0.9	Exponential
Village I	2	0.4	Exponential
Village II	2	0.5	Exponential
Village III	2	0.6	Exponential
Village IV	2	0.7	Exponential
Village V	2	0.8	Exponential

Table 4. Sensitivity of land use types to threat factors.

Land Cover	Habitat Suitability	Threat Sensitivity								
		Rd	Crp	Fld	Cnstrct	V-I	V-II	V-III	V-IV	V-V
Crop	0.3	0.6	0	0.4	0.6	0.6	0.6	0.75	0.8	0.9
Woodland	0.9	0.65	0.6	0.9	0.75	0.5	0.55	0.65	0.7	0.8
Shrub	1	0.6	0.5	0.6	0.8	0.5	0.5	0.55	0.6	0.7
Spares Woodland	0.8	0.7	0.6	0.7	0.8	0.6	0.6	0.75	0.8	0.9
Field	0.3	0.5	0.4	0	0.7	0.5	0.55	0.6	0.65	0.7
Grassland	0.6	0.5	0.6	0.5	0.65	0.6	0.6	0.75	0.8	0.9
Water	0.7	0.4	0.45	0.45	0.7	0.45	0.45	0.55	0.6	0.7
Construction	0	0	0	0	0	0	0	0	0	0
Unused Land	0.35	0.2	0.15	0.3	0.3	0.2	0.2	0.35	0.4	0.5

Note: The habitat suitability values indicate the relative suitability of each land cover type for supporting high-quality habitat, while the threat sensitivity values denote the degree to which each land cover type is affected by specific threats. (Rd = road, Crp = crop, Fld = field, Cntrct = construction, V-I = Village I, V-II = Village II, V-III = Village III, V-IV = Village IV, V-V = Village V).

(4) Calculation of the habitat quality index

The habitat quality index was calculated using the following formula [41,42]:

$$Q_x = \frac{H_x}{H_x + D_x + k}$$

where Q_x is the habitat quality index for a specific location, H_x is the habitat suitability score (indicating the inherent ability of a location to support habitat quality), D_x is the habitat degradation index (reflecting the cumulative impact of all threat factors on habitat quality), and k is the half-saturation constant (controlling the smoothness of the transition of quality values between zero (poor habitat quality) and one (high habitat quality)).

The habitat suitability score (H_x) was derived from the sensitivity of different land use types to various threat factors (Table 3). The habitat degradation index (D_x) was computed by integrating the weights and spatial decay types of the identified threat factors, using the maximum impact distances obtained from the analysis. These maximum impact distances were crucial in determining how far the effects of each threat factor extended spatially, thereby influencing the calculation of degradation.

To classify habitat quality into different levels, the equidistance method was employed. This method categorized the habitat quality index (Q_x) into five distinct levels: lowest (<0.2), low (≥0.2 and <0.4), medium (≥0.4 and <0.6), high (≥0.6 and <0.8), and highest (≥0.8) [43].

After calculating the habitat quality index (Q_x) and identifying areas with varying habitat suitability and degradation levels, the next step involved assessing the spatial patterns of habitat quality across the landscape.

3.3. Spatial Autocorrelation Analysis

To further analyze the spatial distribution of habitat quality, Moran's I statistic was employed to identify clustering patterns [44,45]. Both Global Moran's I and Local Moran's I were utilized to provide a comprehensive analysis of spatial dependencies across the landscape. Global Moran's I was applied to measure the overall spatial autocorrelation of habitat quality throughout the study area. This global measure assesses whether habitat quality values are randomly distributed or exhibit a pattern of spatial clustering. A statistically significant Global Moran's I value indicates a non-random spatial distribution, suggesting that similar habitat quality values tend to cluster together [43]. Local Moran's I was used to identify specific clusters and spatial outliers, such as high–high clusters (areas of high habitat quality surrounded by similar areas of high habitat quality) and low–low clusters (areas of low habitat quality surrounded by similar areas of low habitat quality). This local indicator of spatial association (LISA) allows for the detection of localized patterns of spatial clustering or dispersion that may not be apparent from the global analysis alone.

The spatial autocorrelation analysis was conducted using a 1 km × 1 km grid across the study area in ArcGIS 10.8 [46]. The 1 km grid size was chosen to balance the resolution of the analysis with computational efficiency, providing sufficient detail to capture spatial patterns while maintaining manageable data processing requirements, as well as to maintain consistency in reporting the results. A finer grid could offer more precise local patterns but would significantly increase computational load, whereas a coarser grid might overlook important spatial details.

To create the spatial weights matrix required for Moran's I calculations, an inverse distance weighting approach was used, assigning higher weights to closer habitat patches to reflect stronger spatial interactions. This approach ensured that the analysis adequately captured local spatial dependencies, which are critical for understanding the distribution of habitat quality throughout the landscape. By applying both Global and Local Moran's I, this study aimed to identify the presence of spatial autocorrelation in habitat quality and detect specific clusters to inform targeted conservation strategies. The identification of high-quality clusters highlights areas where conservation efforts should be prioritized, and

the identification of low-quality clusters highlights areas where restoration efforts should be prioritized.

3.4. Establishment of Risk Assessment Model for Human–Elephant Conflicts

Building on the spatial analyses of habitat quality, this section focuses on developing a risk assessment model for human–elephant conflicts. Understanding how these conflicts correlate with habitat conditions and land use patterns is critical for effective conservation planning and conflict mitigation.

3.4.1. Data Collection and Sources

To develop a comprehensive risk assessment model, this study utilized data collected from two primary sources spanning different time periods. For the period from 2010 to 2016, data were obtained from insurance claim records provided by insurance companies. These records detailed incidents involving Asian elephants, including the locations of impacted households, dates of incidents, and types of losses (e.g., damaged crop areas, tree species affected, livestock losses, casualties, and property damage) [29,47]. This dataset was instrumental in understanding the spatial and temporal distribution of human–elephant conflicts during this timeframe. For the period from 2016 to 2022, additional data were extracted from the published literature, focusing on studies documenting human–elephant conflict incidents and their impacts. This dataset provided insights into the proportion of different land types affected by conflicts, such as cropland, forest areas, and other land use categories. By combining these two data sources, we were able to conduct a detailed analysis of how human–elephant conflicts impacted various land use types over different periods.

3.4.2. Identification and Spatial Analysis of Conflict Points

The collected conflict data were georeferenced to specific villages, leading to the identification of 339 human–elephant conflict points across the study area. These spatial data points were essential for pinpointing the areas most affected by Asian elephants and for analyzing the spatial patterns of conflicts over time. The distribution of these conflict points provided critical insights into the areas most vulnerable to human–elephant conflicts, aiding in targeting conservation efforts.

3.4.3. Risk Assessment Model Development

To assess the risk of human–elephant conflicts, the analysis drew on previous research findings indicating that conflicts predominantly occur in croplands, low-slope areas, and sparsely wooded regions adjacent to croplands [29]. A 1 km $\times$ 1 km fishnet grid was created in ArcGIS 10.8, serving as the foundational unit for analysis [46]. The model incorporated cropland data from 2020, applying the natural breaks (Jenks) classification method to categorize the proportion of cropland and establish thresholds for different levels of conflict risk. These were grouped into four risk grades: no risk [0–0.1094), low risk [0.1094–0.3336), medium risk [0.3336–0.6362), and high risk [0.6362–1] [48].

Additional spatial layers, such as sparsely wooded areas adjacent to high-risk zones and slope data, were integrated to refine risk area definitions [29,49]. Areas with a higher likelihood of conflicts were identified based on their proximity to cropland and lower slope gradients. The spatial join tool in ArcGIS linked conflict records to grid units, enabling the calculation of conflict points within each risk area.

3.4.4. Model Validation and Accuracy

The risk assessment model was validated using spatial overlay analysis to evaluate its accuracy. The validation compared model-predicted high-risk areas with actual conflict points from field data. The spatial join tool in ArcGIS was used to calculate the percentage of actual conflict points that fell within the predicted high-risk zones. Further, the Receiver Operating Characteristic (ROC) curve and the Area Under the Curve (AUC) metrics were

employed to assess the model's predictive power and accuracy [50]. The ROC curve visually represented the model's ability to differentiate between high-risk and low-risk areas, while the AUC metric quantified the overall accuracy of the model's predictions.

3.5. Development of Conservation Planning Strategies

Based on the findings from habitat quality assessments and human–elephant conflict risk analyses, this study developed conservation strategies to mitigate conflicts and enhance habitat connectivity in Xishuangbanna. The study area was divided into three zones: Ecological Source Areas, which are high-quality habitats prioritized for protection; Ecological Restoration Zones, which require habitat restoration to improve ecological conditions; and Ecological Transition Zones, which serve as buffers to reduce conflicts between high-quality habitats and human settlements. To enhance landscape connectivity and facilitate the safe movement of Asian elephants, ecological corridors were strategically planned using GIS tools to connect fragmented habitats while avoiding high-conflict and low-quality zones. These corridors were designed to minimize disturbances and promote connectivity among key conservation areas, including the Mengyang, Mengla, and Shangyong reserves. Restoration zones were identified near conflict hotspots and targeted for reforestation and habitat enhancement to improve degraded areas. Conservation strategies aim to optimize habitat quality, enhance landscape connectivity, and mitigate human–elephant conflicts, supporting the long-term survival of Asian elephants and maintaining the ecological integrity of the region.

4. Result

4.1. Assessing Habitat Degradation and Human–Elephant Conflict Risk Using InVEST and GIS-Based Models

Using the InVEST model, this study integrates land use and land cover data, spatial distributions of threat factors, and their respective weights and maximum impact distances to calculate habitat degradation [22]. Key threat factors, including cropland, construction land, orchards, roads, and village development levels, were identified for their significant impact on habitat quality [26,27]. The Normalized Difference Vegetation Index (NDVI) was employed to refine the maximum impact distances for these factors, providing a more precise analysis of their spatial influence on habitat conditions [23,51]. Furthermore, Moran's I spatial autocorrelation analysis was applied to identify clusters of high habitat and low habitat quality, offering insights into the spatial patterns that can guide conservation priorities [24].

Additionally, a GIS-based conflict risk model was developed using insurance claim data to simulate human–elephant conflict risk levels across the study area. The claim data include the location and extent of damage and hence are a good measure of conflict risk and impact.

4.2. Habitat Quality Assessment

The spatial distribution of habitat degradation and scarcity across the study area shows a heterogeneous pattern, with both high and low degradation levels observed (Figure 3). Establishing habitat degradation in the InVEST model involves mapping the impact of threats (roads, cropland, etc.) on the existing landcover; it is not a reflection of the change in habitat over two points in time. Higher degradation is predominantly found in the central and southern regions, where intensive land use and human activities are concentrated, particularly around high-grade administrative villages, croplands, and orchards. These areas exhibit degradation levels reaching up to 0.164, suggesting significant ecological stress. In contrast, the northern region generally displays lower degradation levels, indicating less impact from anthropogenic activities.

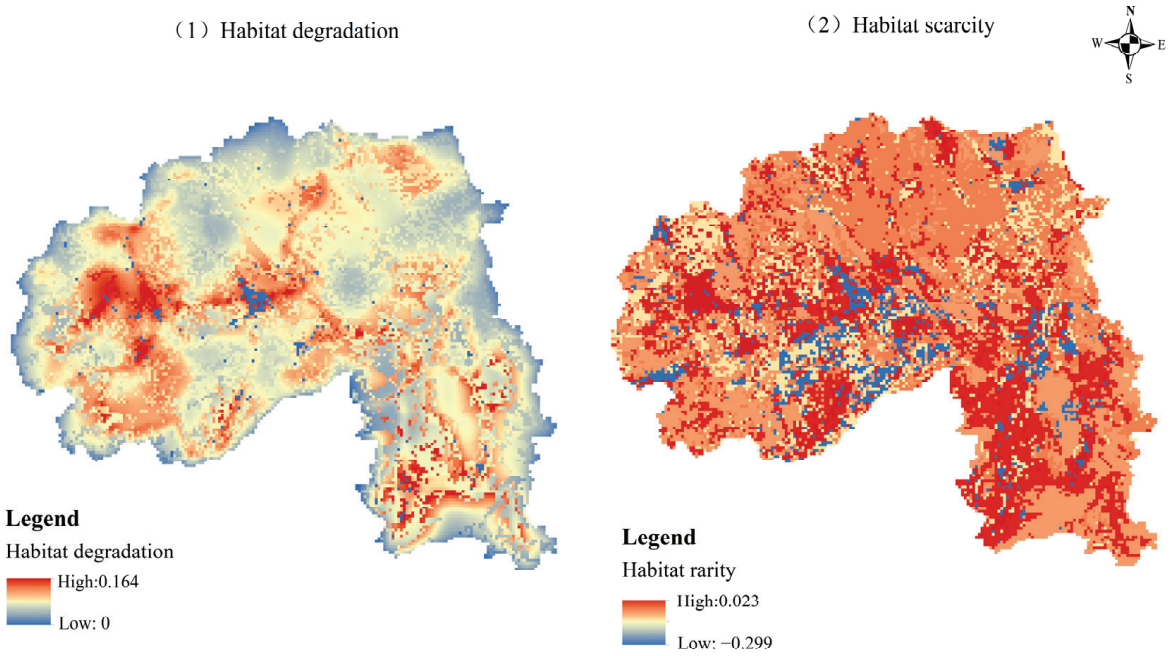

Figure 3. Spatial distribution of habitat degradation and habitat scarcity in Xishuangbanna.

Habitat scarcity is also notably high throughout the study area, particularly in the western and southern regions. These regions are characterized by both high degradation and high scarcity, identifying them as vulnerable areas that might require urgent ecological protection measures. The central region shows lower habitat scarcity but is adjacent to high degradation zones, suggesting a potential risk for further ecological decline.

The analysis of habitat quality indicates an average habitat quality index of 0.4191 across the study area, reflecting a moderate level of overall habitat quality. The spatial distribution of habitat quality (Figure 4) reveals that low-grade habitats (quality scores below 0.4) dominate the landscape, accounting for 51.58% of the total area. The lowest quality class (scores below 0.2) spans 3427 km^2, or 17.90% of the study area, while the highest quality class (scores above 0.8) is limited to 992 km^2, representing 5.18% of the area (Table 5).

Table 5. Area and proportion of different habitat quality classes (year 2020).

Habitat Quality Status	Score Range	Area (km^2)	% of Total Area
Lowest	<0.2	3427	17.90
Low	≥0.2, <0.4	6447	33.68
Medium	≥0.4, <0.6	4513	23.58
High	≥0.6, <0.8	3763	19.66
Highest	≥0.8	992	5.18

Higher habitat quality is generally observed in the northern region, whereas the southern and central regions exhibit lower-quality habitats. The lowest-quality areas are primarily found along major roads, particularly in the southeastern and southwestern parts of the study area. These regions are in close proximity to orchards, high-grade administrative villages, and croplands, indicating a clear correlation between intensive land use and reduced habitat quality.

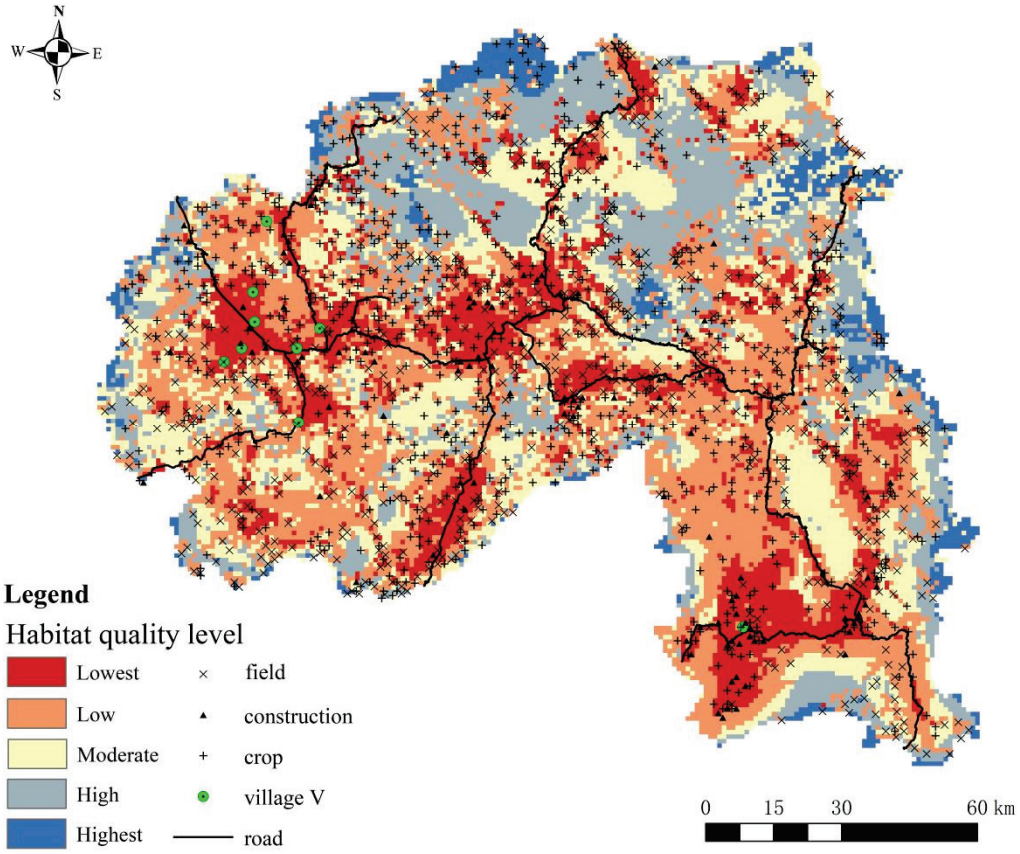

Figure 4. Spatial distribution of habitat quality in Xishuangbanna.

4.3. Risk Assessment of Human–Elephant Conflicts

The risk assessment of human–elephant conflicts (HEC) across Xishuangbanna identified significant spatial patterns in the distribution of conflict points, derived from insurance claim data and the literature as described earlier, and analyzed using spatial methods. The spatial distribution map (Figure 5) shows that conflicts are predominantly concentrated around key protected areas, including Mengyang (MY), Mengla (MLa), and Shangyong (SY), as well as along major roads and in regions with high levels of human activity. Areas with no risk account for 68.35% of the total study area (13,084 km^2), while low-risk areas account for 17.40% (3330 km^2), medium-risk areas for 10.46% (2003 km^2), and high-risk areas for 3.79% (725 km^2) (Table 6). Although high-risk areas are relatively small in size, they exhibit a high frequency of conflicts and generally lower habitat quality. Zones with a high frequency of conflict were identified in the western, southeastern, central, and northern regions of Xishuangbanna, with these areas characterized by proximity to agricultural lands (particularly croplands) and densely populated human settlements. The data indicate that conflicts are more prevalent where natural habitats intersect with agricultural and developed lands, with areas near croplands and adjacent to protected areas reporting higher conflict rates due to elephants moving into these regions, resulting in crop damage and other human–elephant interactions.

The risk assessment model demonstrated strong predictive accuracy, correctly identifying approximately 87% of high-risk zones and achieving a Receiver Operating Characteristic-Area Under Curve (ROC-AUC) score of 0.9, which indicates excellent model performance [52]. The sensitivity analysis further validated the model's robustness, showing consistent results under varying parameter settings. These results confirm the model's capability to accurately identify areas at high risk for human–elephant conflicts, providing a reliable foundation for future conflict mitigation strategies.

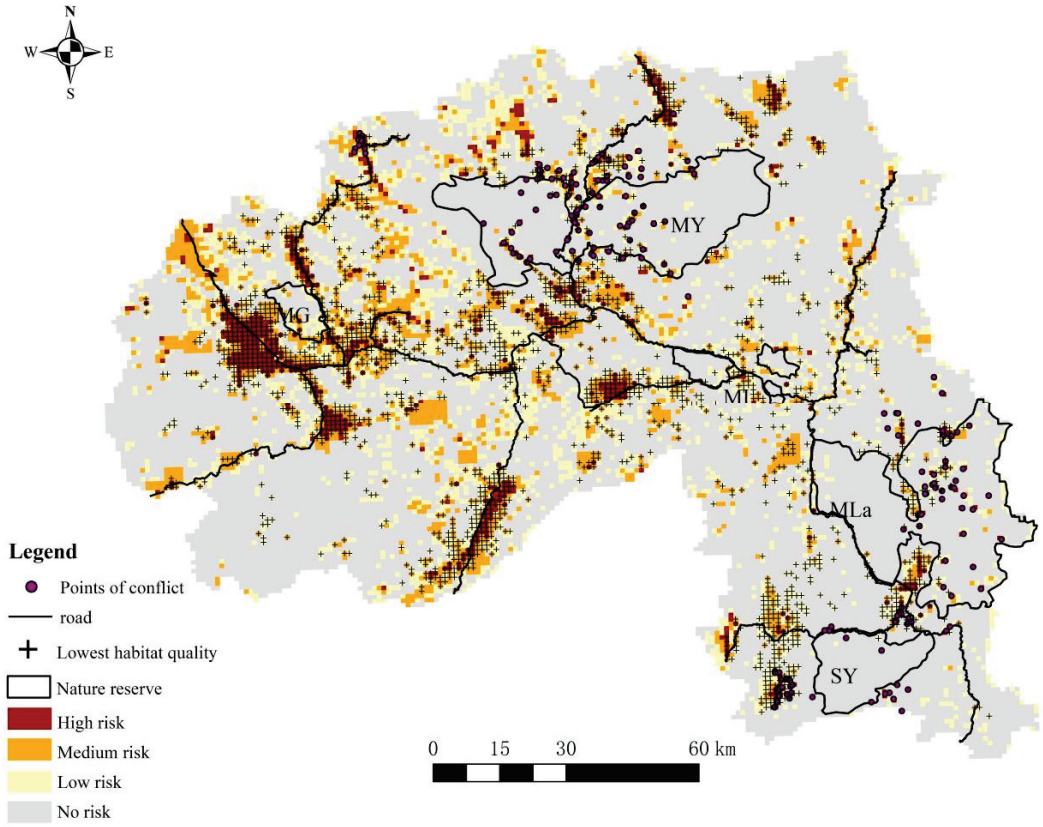

Figure 5. Spatial distribution of human–elephant conflict (HEC) risk in Xishuangbanna (MG = Mangao, MY = Mengyang, ML = Menglun, MLa = Mengla, SY = Shangyong).

Table 6. Area and proportion of different human–elephant conflict (HEC) levels (year 2020).

Risk Class	Area (km^2)	% of Total Area
No risk	13,084	68.35
Low risk	3330	17.40
Medium risk	2003	10.46
High risk	725	3.79

4.4. Integration of Habitat Quality and Conflict Risk Models for Conservation Planning

The integration of habitat quality and human–elephant conflict (HEC) risk models offers a robust foundation for conservation planning in Xishuangbanna, pinpointing areas where interventions are most urgently needed. Spatial analysis reveals a notable overlap between high-risk HEC zones and regions of low habitat quality, particularly in the western, southeastern, central, and some northern parts of the study area. These high-risk zones are primarily located around key protected areas, such as the Mengyang (MY), Mengla (MLa), and Shangyong (SY) reserves, where there is a significant intersection between human activities and elephant habitats. The HEC risk map indicates that approximately 90% of conflict points are situated within designated risk zones, highlighting the need for targeted management strategies in these areas (Figure 5).

Further spatial analysis using Moran's I reveals that high-quality habitats which form high–high spatial clusters are predominantly located in the northern and peripheral regions near protected areas such as Mengyang (MY). These areas, identified as Ecological Source Areas, are prioritized for strict protection to maintain ecological integrity (Figure 6). In contrast, areas categorized as low–low spatial clusters, which indicate substantial habitat degradation, are concentrated around Shangyong (SY), Mangao (MG), and Menglun (ML). These zones, characterized by low habitat quality and high conflict risk, are designated as

Ecological Restoration Zones, necessitating focused restoration efforts to enhance habitat conditions and mitigate human–elephant conflicts (Table 7, Figure 6). High–high clusters are areas of high habitat quality surrounded by similar areas of high habitat quality. Low–low clusters are areas of low habitat quality surrounded by similar areas of low habitat quality. High–low outliers are areas of high habitat quality surrounded by contradictory areas of low habitat quality. Low–high outliers are areas of low habitat quality surrounded by contradictory areas of high habitat quality.

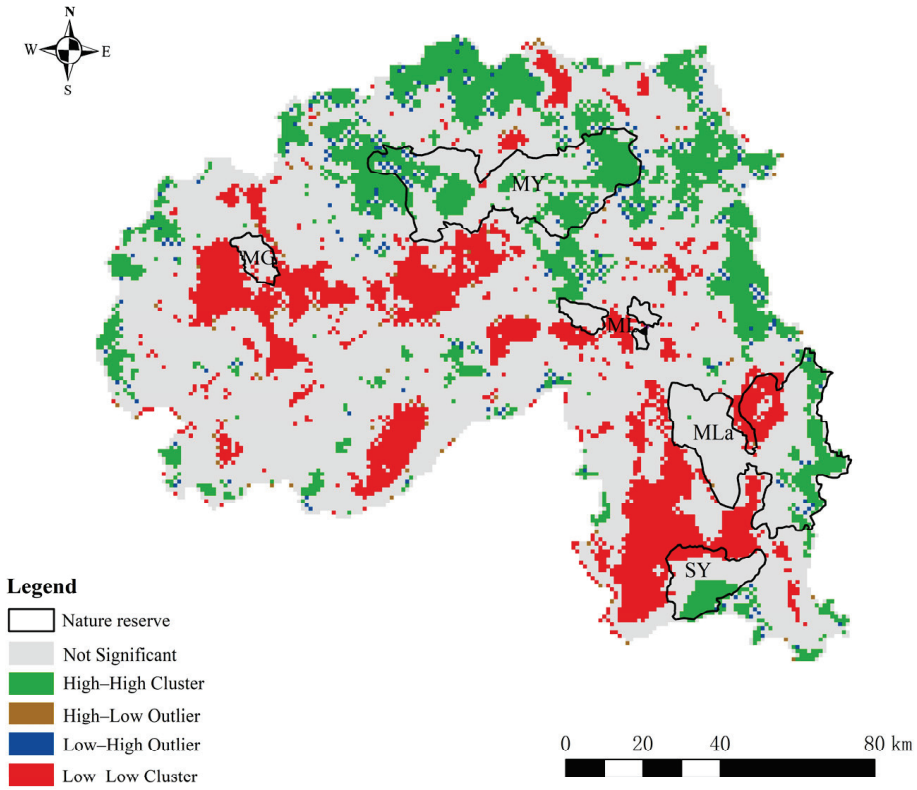

Figure 6. The spatial clustering of different habitat quality levels, highlighting the locations of high–high clusters near the Mengyang protected areas and low–low clusters in the western and south-eastern regions. (MG = Mangao, MY = Mengyang, ML = Menglun, MLa = Mengla, SY = Shangyong).

Table 7. Area and proportion of local spatial autocorrelation of habitat quality (year 2020).

Local Spatial Autocorrelation	Area (km^2)	% of Total Area
Not Significant	12,607	65.86
High–High Cluster	3144	16.42
Low–Low Cluster	3058	15.98
High–Low Outlier	81	0.42
Low–High Outlier	252	1.32

Additionally, integrating habitat quality and conflict risk data is instrumental in planning ecological corridors to enhance habitat connectivity while minimizing conflict risk (Figure 7). These corridors are strategically mapped to connect high-quality habitats, such as those in Mengyang (MY), Mengla (MLa), and Shangyong (SY), while avoiding the high-risk zones identified in the conflict risk model. This strategic placement supports the safe movement of elephants and reduces landscape fragmentation, aligning with conservation goals to protect biodiversity, improve habitat connectivity, and minimize human–elephant conflicts.

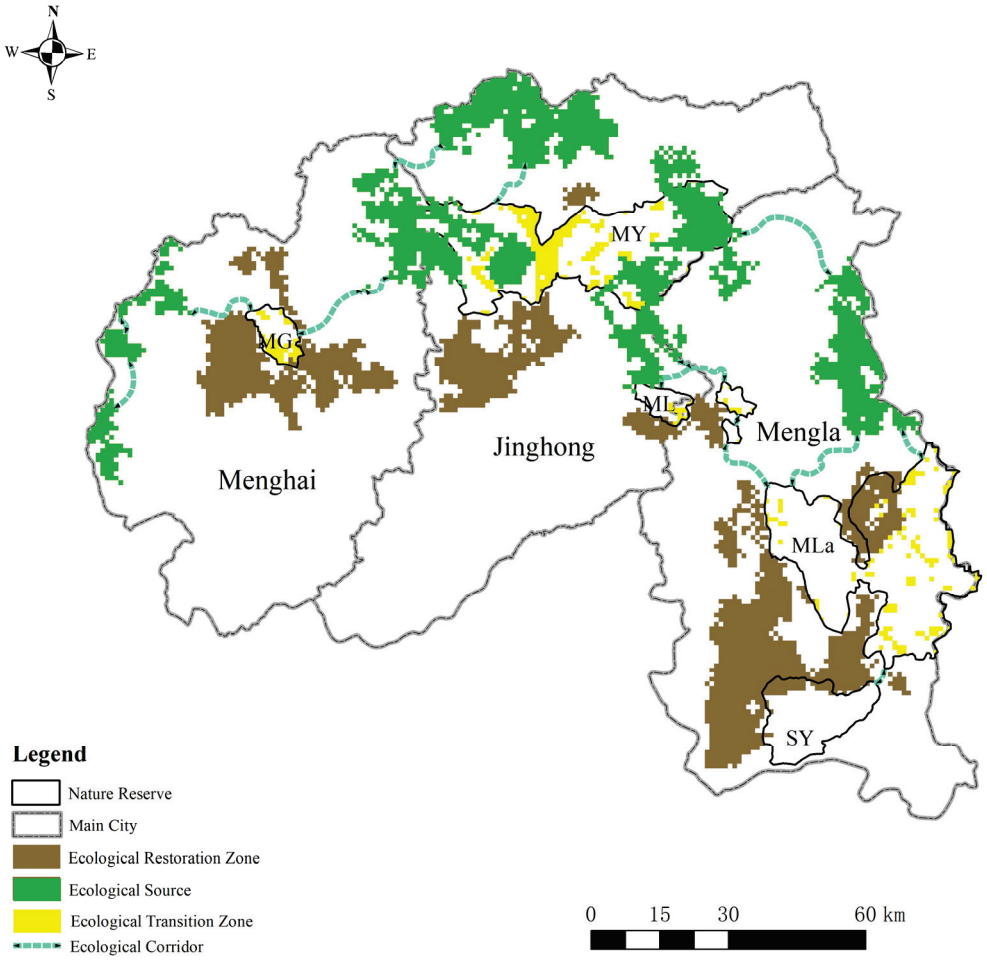

Figure 7. Proposed ecological corridors with strategic placement to avoid areas with high conflict risk and to maximize habitat connectivity between protected areas. (MG = Mangao, MY = Mengyang, ML = Menglun, MLa = Mengla, SY = Shangyong).

5. Discussion

Globally, wildlife and biodiversity conservation has become an increasingly urgent issue. With the expansion of human activities, wildlife habitats and biodiversity face severe challenges [53]. Xishuangbanna, located in Yunnan, China, is a critical tropical rainforest reserve essential for biodiversity conservation, particularly for the Asian elephant [15,54]. However, expanding human activities have led to habitat degradation and increased human–elephant conflicts in the region [16,55]. This study provides new insights into these challenges by integrating habitat quality assessments with the spatial analysis of conflict risks, offering a novel framework for conservation planning.

Human activities, including urbanization, agriculture, and infrastructure development, are the primary drivers of large-scale ecological disturbances in Xishuangbanna. Our findings highlight that agricultural expansion for cash crops (e.g., rubber and tea) and infrastructure development are key contributors to habitat degradation and human–elephant conflicts. For example, the conversion of forest lands in agricultural areas and the construction of roads to service these areas is an issue. These roads cut into habitats and corridors, driving fragmentation. This fragmentation in turn impedes natural elephant movement and increases human–wildlife interactions. This is backed up by our spatial analysis, which revealed significant habitat fragmentation and clusters of low-quality habitats near high-conflict zones, particularly in areas adjacent to reserves such as Mengyang, Mengla, and Shangyong. These results align with previous studies showing that agricultural intensification reduces forest cover and fragments habitats, intensifying human–wildlife conflicts [56,57].

Moreover, habitat fragmentation is exacerbated by infrastructure projects, such as constructing roads to increase human accessibility to remote areas. This disrupts elephant movement corridors, creating ecological traps [26,58]. Elephants are often attracted to human-dominated landscapes due to the availability of high-energy crops such as rubber, tea, and rice, leading to frequent conflicts [16,59]. These interactions underscore the urgency of the need for strategies that mitigate the dual challenges of habitat degradation and human–elephant conflicts.

The concept of disturbance regimes—i.e., the patterns and intensities of disruptions, both natural and anthropogenic, to ecosystem structure, function, and biodiversity—is vital for understanding the cumulative impacts of human activities on ecosystems [60]. Agricultural and infrastructure developments in Xishuangbanna have fundamentally altered disturbance regimes, as evidenced by our spatial analysis. The InVEST model indicates that intensive cropland use and proximity to roads increases habitat degradation indices, leading to ecological thresholds being exceeded. Combining that with our conflict data, we see, for example, areas near the Shangyong and Mengla reserves exhibiting both high human–elephant conflict and low habitat quality. As with this example, this adverse impact on disturbance regimes is particularly evident in areas where high-intensity human activities coincide with poor habitat quality and high conflict risks.

The Intermediate Disturbance Hypothesis further supports these findings, suggesting that moderate disturbances foster biodiversity by creating spatial and resource heterogeneity, whereas when disturbances exceed ecosystem resilience thresholds, as in the case of continuous deforestation for plantations, they lead to irreversible degradation [14]. This study extends this hypothesis by using spatially integrated analysis to demonstrate a link between high-intensity disturbances and increased conflict risks. For instance, the Mengyang reserve is surrounded by dense agricultural activities and road networks. It also shows a high concentration of human–elephant conflict incidents. GIS-based conflict risk models reveal that areas adjacent to croplands with steep degradation gradients are hotspots for such conflicts. The overlap of high-risk conflict zones and low-quality habitat areas, as shown in Figure 5, further supports this connection. These findings highlight the cascading effects of habitat degradation and fragmentation, where reduced habitat quality amplifies the frequency and intensity of human–elephant conflicts.

The innovation of this study lies in the integration of the InVEST model with GIS-based spatial analysis to address conservation challenges in Xishuangbanna. By identifying specific areas where habitat quality is low and conflict risks are high (e.g., Mengyang reserve), this approach provides actionable insights for targeted interventions such as ecological corridors and restoration zones. Unlike conventional methods, this integrated framework quantifies habitat quality and conflict risks simultaneously, offering a more holistic perspective for conservation planning.

However, there are limitations to this study. For instance, using insurance claim data to model conflict risk may not capture all incidents, potentially underestimating the frequency and severity of conflicts. Additionally, relying on village-level development indicators may not fully account for the finer-scale impacts of human activities on habitat quality. Future research should consider more granular data and incorporate additional factors such as climate change, land-use scenario modeling, and socio-economic dynamics to enhance the applicability and predictive accuracy of the model. These enhancements could improve the precision and effectiveness of conservation decisions.

In comparison to other studies, this research offers valuable insights into developing integrated conservation strategies that address both ecological and social challenges. Previous studies indicate that many protected areas face similar challenges, such as habitat loss and wildlife endangerment, as observed in conservation areas in Africa [61,62] and regions in Indonesia, including Borneo [63] and Sulawesi [64]. However, these ecosystems are facing severe degradation due to threats such as logging, oil palm plantations, mining, and forest fires. According to our findings, establishing ESAs, ERZs, and ecological corridors could effectively address these challenges. Furthermore, the InVEST model and

ArcGIS analysis provide a robust platform for sustainable conservation. The InVEST model aids in objectively assessing ecosystem service values and integrates multi-source data, while ArcGIS modeling provides accurate spatial information to support more effective conservation strategies.

6. Conclusions

The integration of habitat quality and human–elephant conflict (HEC) risk models has provided a comprehensive framework for conservation planning in Xishuangbanna, highlighting critical areas where targeted interventions are necessary. The spatial analysis revealed significant overlap between high-risk HEC zones and regions of low habitat quality, particularly around key protected areas, such as the Mengyang (MY), Mengla (MLa), and Shangyong (SY) reserves. These findings indicate that areas with intensive human activity and degraded habitats are at the highest risk for human–elephant conflicts, underscoring the urgent need for focused management strategies in these regions.

By identifying Ecological Source Areas and Ecological Restoration Zones, this study offers a strategic approach to prioritizing conservation efforts. Ecological Source Areas were identified in places of high-quality habitats, mainly situated in the northern and peripheral regions. These require strict protection to preserve their ecological integrity. Ecological Restoration Zones were identified in areas of significant habitat degradation and high conflict risk, as described in Section 4.3. Specifically, areas classified as low–low clusters indicate severe habitat degradation, and are primarily concentrated around Shangyong (SY), Menggao (MG), and Menglun (ML) (Figure 6), with significant overlap with high-risk conflict (Figure 5). These require targeted restoration actions to improve habitat quality and mitigate conflict risks. From these, ecological corridors were proposed to strategically connect high-quality habitats while avoiding high-risk zones. These are crucial for enhancing habitat connectivity and reducing landscape fragmentation, thereby supporting the safe movement of Asian elephants and other wildlife.

This study's findings demonstrate the importance of integrating habitat quality assessments with conflict risk analyses to guide effective conservation planning. By leveraging spatial models and data-driven approaches, conservation efforts can be more precisely targeted, ensuring resources are allocated where they are most needed to achieve both ecological and social objectives. The model validation results, with high predictive accuracy for identifying high-risk areas, provide confidence in the utility of these models for informing future conservation policies and strategies in Xishuangbanna.

In conclusion, this research highlights the critical need for a multi-faceted approach to conservation planning that combines habitat protection, ecological restoration, and conflict mitigation. The integrated use of habitat quality and conflict risk models offers a powerful tool for conservationists and policymakers to prioritize actions that protect biodiversity, enhance habitat connectivity, and foster coexistence between humans and wildlife. Future research should focus on refining these models with more granular data and exploring their applicability in other regions with similar conservation challenges. Ongoing monitoring and adaptive management are essential to respond effectively to changing ecological conditions and human dynamics in Xishuangbanna.

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Prioritising Ex Situ Conservation for Malagasy Mammal Species in Line with IUCN's 'One Plan Approach to Conservation'

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Abstract: Madagascar, as one of the global biodiversity hotspots, hosts numerous unique terrestrial mammal species that need urgent protection. To identify priority species for conservation, an updated list of terrestrial Malagasy mammal species was compiled, including their threat status, distribution, endemism level, Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listing, and Evolutionarily Distinct and Globally Endangered (EDGE) score. An overview of these species kept in zoos worldwide was created using the Zoological Information Management System and Zootierliste to assess ex situ conservation efforts. Nearly 60% of the 212 native terrestrial mammal species are threatened with extinction, with 18% being regional endemics, 39% microendemics, and 42% endemics. The majority of these species (92%) occur within protected areas. About half of Madagascar's mammals are listed under CITES, and less than half have an EDGE score. Only 34 species are kept in zoos globally, with 26 Red-Listed as threatened. Nine out of seventeen families are not represented in zoos. A total of 1545 institutions, primarily in Europe and North America, keep Malagasy mammal species, with successful reproduction reported for 28 species in the last 12 months, 23 of them listed as threatened on the IUCN Red List. To maximize conservation, we recommend reallocating resources towards priority species and implementing concerted ex situ and in situ actions as proposed by the IUCN's One Plan Approach.

Keywords: conservation; ex situ; gap analysis; conservation breeding; protected area coverage; Madagascar

1. Introduction

On a global scale, ongoing anthropogenic influence is currently promoting an extinction rate at least a hundred times higher than estimated during the previous 10 million years [1], with an estimated background extinction rate of 0.1 to 1 extinction per million species per year [2]. Such negative trends are especially concerning for biodiversity hotspots, which are defined by a high level of endemic species while at the same time experiencing a high degree of environmental degradation [3].

To safeguard and conserve endangered species, the International Union for Conservation of Nature's (IUCN) Conservation Planning Specialist Group (CPSG) introduced the One Plan Approach (OPA). This comprehensive conservation strategy combines both ex situ and in situ methods by uniting the knowledge and resources of zoological institutions and wildlife conservationists inside or outside the species' natural ranges to coordinate efforts for more effective conservation. The aim is to manage wild and held populations as one rather than treating them separately in order to ultimately ensure healthy and genetically diverse populations to counteract their risk of extinction [4,5]. This involves the management of breeding programs and incorporating tools such as studbooks, bringing

individuals into human care to ensure a diverse gene pool, as well as the successful reintroduction of individuals into their natural environment when required. Additionally, in situ conservation is achieved by assessing and addressing risks and threats to wild populations and protecting and restoring ecosystems and habitats. One key component of OPA is the consistent sharing of viable information and data between all stakeholders for collaborative decision-making processes and adaptive management [5]. Zoos have played a vital role in the past in conserving endangered species through breeding programs, especially when in situ methods are difficult due to habitat destruction or illegal human activities such as poaching [6]. With the intensifying threats to global biodiversity, zoos could become an even more important instrument as a reserve for species in the future [6,7].

Due to its long geographic isolation from the main African continent [8], Madagascar is known for its unique biodiversity and is described as one of the most important biodiversity hotspots [9,10], with an increase in newly discovered and described species in the last years [11,12]. The country is also one of the few that still has the potential to discover new mammal species [13,14]. A prominent example is the lemur genus *Microcebus*, the smallest primate in the world, with a growing number of newly described species [13,15].

A recent assessment estimated the overall rate of endemism in Malagasy land vertebrates at 84% with a high rate of endemism in mammal species at 95.5% [12]. Of all families described of extant terrestrial mammals in Madagascar, all nonvolant are endemic, namely Cheiroglaeidae, Daubentoniidae, Eupleridae, Indriidae, Lemuridae, Lepilemuridae, Nesomyidae, Soricidae, and Tenrecidae [16]. The most species-rich order is lemurs, a primate order unique to Madagascar [17]. Worldwide, mammals are among the most threatened vertebrate taxa, as 30% of terrestrial mammal species show population declines [18], and 26% of mammal species are threatened with extinction [19]. Madagascar is a region with a predicted high risk of extinction for mammals [20].

The island harbors seven main ecoregions: mangroves along the west coast, subhumid forest and ericoid thickets in the central parts, lowland forest in the eastern parts, dry deciduous forest in the west, succulent woodlands in the southeast, and spiny thickets in the southern region [21]. The highest species richness and levels of endemism can typically be found in the humid forest [11]. Despite growing conservation efforts in the last two decades, the establishment of numerous protected areas, and 10.4% of the island´s area being under protection [22,23], Madagascar´s natural forest decreased by 25% between 2001 and 2021 [24]. As most endemic vertebrates on the island are dependent on forests [22,25], deforestation and forest fragmentation pose another major risk to the survival of Malagasy species [26], including mammals [27]. Furthermore, species face a multitude of other threats, including overexploitation, destructive agriculture techniques, invasive species, and diseases [23], making the island one of the global conservation priorities [9,28–30]. Since undiscovered species in general, and mammals living in the tropics specifically, have an increased risk of extinction [31] and considering the continued threat for already described Malagasy mammal species, holistic conservation plans are needed [23].

In order to support further conservation measures for terrestrial Malagasy mammals, a comprehensive species list was compiled in order to provide input into conservation prioritization with respect to the One Plan Approach and give a guideline, especially for zoological institutions, to ensure the survival of highly threatened species. For this overview, we compiled data on whether animals are held and bred successfully in zoos, their threat and population status, legal protection, coverage by protected areas, and existing prioritization status according to their evolutionary distinctiveness.

2. Materials and Methods

2.1. Species List and Threat Status

A list of terrestrial mammals in Madagascar was compiled according to the latest assessment of the IUCN Red List of Threatened Species [19]. The list was supplemented and reviewed according to the chapter 'Introduction to Mammals' in *The New History of*

Madagascar by Goodman (2022) [16]. Introduced species were excluded. Subspecies were not considered separately in the analysis.

Information acquisition regarding the threat status and population trends for each species was extracted from the IUCN Red List of Threatened Species. Species classified as Vulnerable (VU), Endangered (EN), and Critically Endangered (CR) were identified as 'threatened'. Population trends in the wild for each species were categorized into increasing population (↑), decreasing population (↓), stable population (-), and unknown (?) [19].

2.2. Distribution

A biogeographical map illustrating the various ecological regions of Madagascar was generated using shapefiles from the World Wildlife Fund [32] originating from the study by Olson et al. (2001) [21]. The open-source software QGIS version 3.22.8 LTR [33] was employed to determine the occurrences of terrestrial mammal species in the seven ecoregions of Madagascar based on distribution data of the species by the IUCN (2023) [19].

For categorizing species into microendemics, regional endemics, (national) endemics, or widespread, we compared IUCN distributions of all species with the center of endemism proposed by Wilmé et al. (2006) [34] (Figure 1). Microendemics were defined as species that overlap only with one center of endemism or which have an area of occurrence smaller than 1000 km^2. Regional endemics were defined as species that overlap with two centers of endemism. Endemics are restricted to Madagascar but overlap with three or more centers of endemism. Widespread species also occur outside of Madagascar.

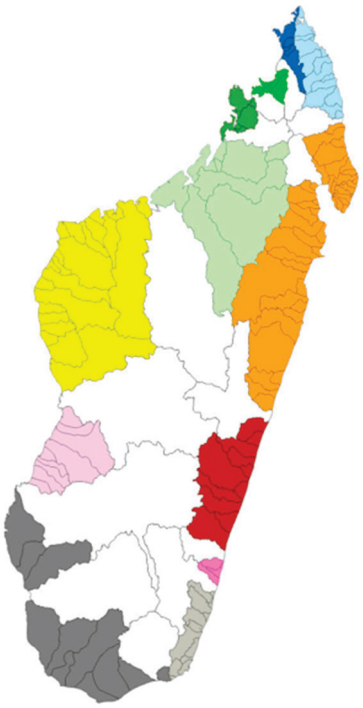

Figure 1. Centers of endemism in color. Regions without centers of endemism in white. Based on Wilmé et al. (2006) [34].

The information on distribution areas for the terrestrial Malagasy mammal species relies on data provided by the IUCN (2023) [19]. The shapefiles of the distribution for each terrestrial Malagasy mammal species were specified using ArcGIS Pro 3.0.0 [35] and the geographical data of the centers of endemism by Wilmé et al. (2006) [34].

2.3. ZIMS and "Zootierliste"

To assess Malagasy mammal species in zoological institutions, information was obtained from the Zoological Information Management System (ZIMS) database maintained

by Species360 [36]. The analysis of ZIMS encompassed the overall count of institutions per region, including the total number of males, females, and individuals of unspecified sex kept within each institution. Furthermore, the reproductive success of each species within the past 12 months, along with the corresponding number of participating institutions, was determined. Lastly, possible conservation breeding programs such as the European Studbook (ESB), the EAZA Ex situ Programme (EEP) of the European Association of Zoo and Aquaria, and the Species Survival Plan (SSP) of the Association of Zoos and Aquariums in North America were documented. To evaluate conservation gaps, the number of species kept in the past and present were identified. As a zoo is not obligated to participate in ZIMS, a 100% complete data collection is not available. To further complete the data set on terrestrial Malagasy mammals, information on former and present keeping was gathered from the website 'Zootierliste' (List of Zoo Animals, ZTL). ZTL provides data about vertebrate species in European zoos and other public and private animal institutions covering recent and past keepings. This information system is managed by zoos and private citizens and does not contain information about the number of individuals of each species and breeding successes [37]. The analysis of the ZIMS database was conducted on 16 February 2024 and of the ZTL platform on 17 February 2024.

2.4. CITES

CITES is a United Nations convention to control legal wildlife trade better and to protect endangered species from extinction. The main source for compliance is the CITES appendices. Included species have been evaluated to determine whether international trade would pose a threat to their survival. The appendices include more than 40,000 species with different protection levels. Under Appendix I, species are listed which are prohibited from being traded internationally. Appendix II covers the trade of species that could become endangered unless controlled. Therefore, permits are needed for each step in the trade, ranging from export to import and transport. Finally, Appendix III records species that are protected in at least one member nation [38]. The CITES appendices were scanned on 18 February 2024 in order to determine the listings for each terrestrial Malagasy mammal species.

2.5. EDGE Score

EDGE species are animal species that are considered exceptional, distinct, and frequently neglected in conservation programs. The EDGE of Existence program recognizes species with an exclusive evolutionary pathway and a high risk of extinction and was established by the Zoological Society of London. Based on a phylogenetic analysis representing the Evolutionary Distinctiveness and the IUCN Red List Categories of the threat status, the EDGE score is calculated for each species. A high EDGE score indicates that the species has a limited number of closely related species and is threatened with extinction, therefore needing immediate conservation action. The program aims to conserve unique species and safeguard the world´s biodiversity by raising awareness, supporting conservation efforts, and providing educational knowledge [39]. The investigation of the EDGE score for eligible terrestrial Malagasy mammals was performed on 6 February 2024.

2.6. Prioritization

To determine which species needs special attention in conservation measures a prioritization list was compiled. We first prioritized all terrestrial Malagasy mammal species that are not kept in zoos. The second prioritization criterion was the level of endemism with higher importance for species that are microendemic, followed by regional endemic and endemic. The least prioritized were widespread species i.e., occur outside of Madagascar. Thirdly, the IUCN Red List status was considered with higher prioritization as the threat level increased. Furthermore, the EDGE score was used from highest to lowest as the last criterion for the evaluation.

These prioritization criteria were chosen because they are globally accepted and approved by internationally recognized conservation authorities or organizations (such

as the IUCN). Furthermore, they are widely accessible to the conservation community. Weighting was considered, but we have decided against it due to the different scorings (e.g., numerical score vs. a small number of categories). A disadvantage of an index created by weighting is that details are lost that may be crucial for decisions. In conservation, decisions need to be taken on a participatory level, hence the weighting should happen on a strategic level, not a scientific level.

2.7. Protected Area and Key Biodiversity Area Coverage

Based on our species list, we used the rredlist package for R [40] to extract detailed information on preferred habitats from the IUCN Red List, matching the identical classes of a habitat availability map with a spatial resolution of 100 m [41]. Preferred habitats of each species were intersected with general range estimates provided by the IUCN Red List, and the resulting presence–absence maps were further intersected with the protected area network obtained from www.protectedplanet.net (accessed on 20 July 2022) and key biodiversity areas (KBAs) [42]. KBAs are critically important sites for the global persistence of biodiversity, identified based on their significance for the conservation of species and ecosystems [43]. Species richness maps accounting for habitat availability were computed by stacking the single presence–absence maps. Following Crisp et al. (2001) [44], regions of high local endemism were identified using the corrected weighted endemism approach, which balances local species richness and the proportion of species occupying small geographic ranges.

3. Results

3.1. Species List and Threat Status

Of the 212 native terrestrial Malagasy mammal species that were reported, a total of 127 were evaluated as threatened according to the IUCN: 39 Vulnerable, 55 Endangered, and 33 Critically Endangered. The number of non-threatened species was 72, including 70 Least Concern and 2 Near Threatened species. Approximately 6% (N = 13) of terrestrial mammals of Madagascar were Data Deficient [19] (Figure 2). The evaluation of the population status of terrestrial Malagasy mammals revealed that 142 species had declining populations, 8 species had stable populations, and only 1 species showed an increasing population trend. For the remaining 61 species, the population status was 'Unknown' [19].

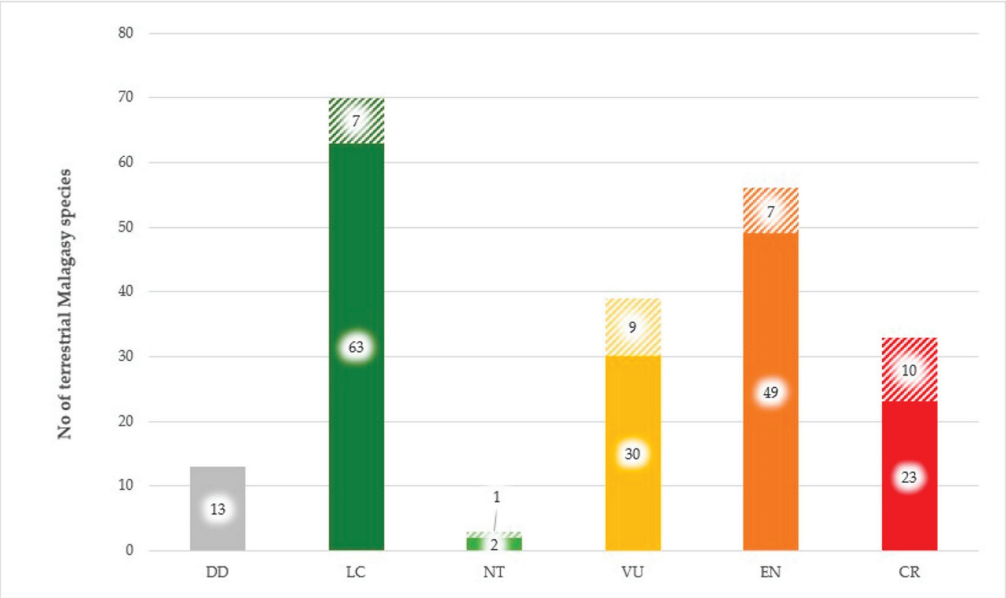

Figure 2. IUCN Red List status of terrestrial Malagasy mammals [19]. Species kept in zoos in stripes. DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

3.2. Distribution

The occurrences of terrestrial mammals in the seven biogeographical regions of Madagascar differed. Most of the species inhabited the subhumid forest (N = 149), followed by lowland forest (N = 134), dry deciduous forest (N = 112), ericoid thickets (N = 65), spiny thickets (N = 61), and succulent woodland (N = 50). The least number of terrestrial Malagasy mammal species were present in the mangroves along the west coast (N = 46) (Figure 3). With 78% (N = 165), the majority of the 212 species occurred in more than one, and only 5% (N = 12) lived in all seven biogeographical regions of Madagascar.

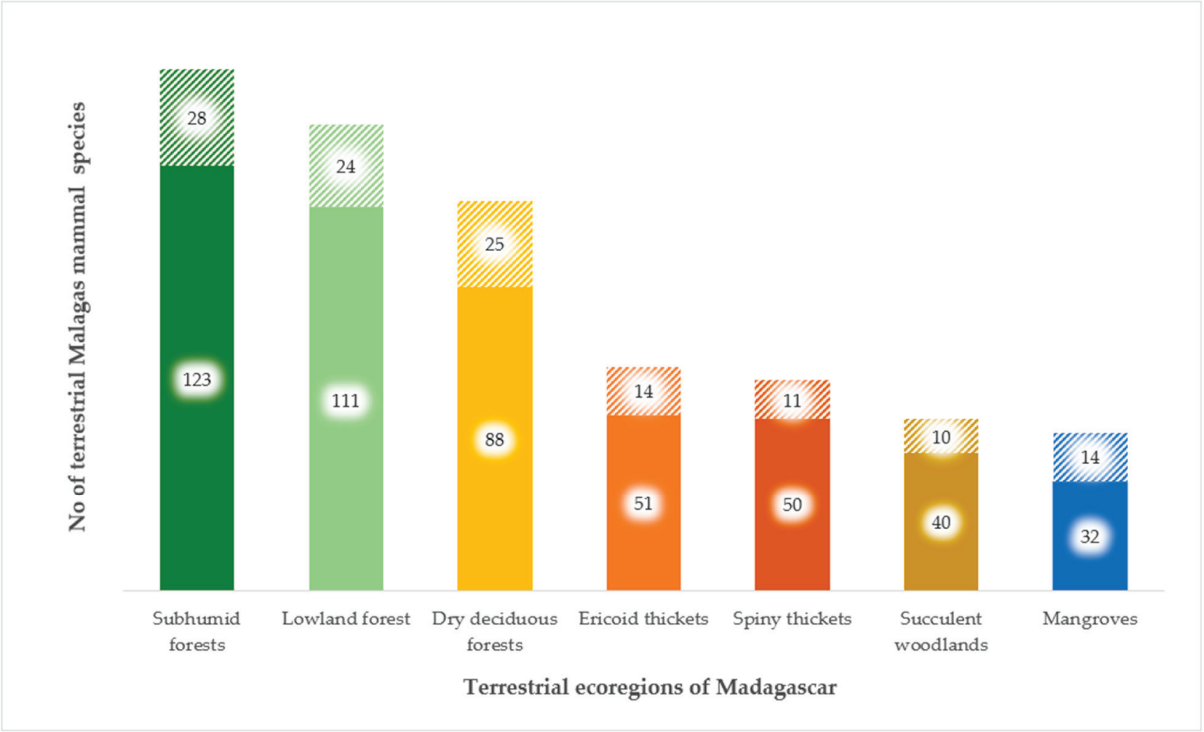

Figure 3. Occurrences of terrestrial Malagasy mammal species in different biogeographical regions of Madagascar. Species kept in zoos in stripes. Species may occur in more than one region.

The biogeographic analysis considering the level of endemism showed that only 4 of the 212 terrestrial Malagasy mammal species were also distributed outside of Madagascar and, therefore, evaluated as 'widespread'. All four were bat species, one species each of the family Hipposideridae and Molossidae, and two species of the family Miniopteridae. Most of the terrestrial mammal species of Madagascar occurred in more than two centers of endemism and are, therefore, endemic with 42% (N = 88). Microendemics with 39% (N = 82) inhabited only one center of endemism or had an area of occurrence under 1000 km^2, followed by regional endemic species with 18% (N = 38) living in two centers of endemism.

3.3. ZIMS and "Zootierliste"

All species that were listed in ZIMS except for two were also documented in ZTL. For 84 species, no records in either database were found. In total, 16% (N = 34) of the 212 terrestrial Malagasy mammal species from 8 different families are presently kept in zoos worldwide (Figures 4 and 5). Of the 127 threatened terrestrial mammal species of Madagascar, 20% (N = 26) and 9% (N = 8) of the 85 non-threatened species were held in zoos. According to IUCN, 28 of the 34 terrestrial Malagasy mammal species in captivity had a declining in situ population trend, while 3 species had a stable population in the wild. For the remaining three species kept in zoos, the population trend was assessed as unknown.

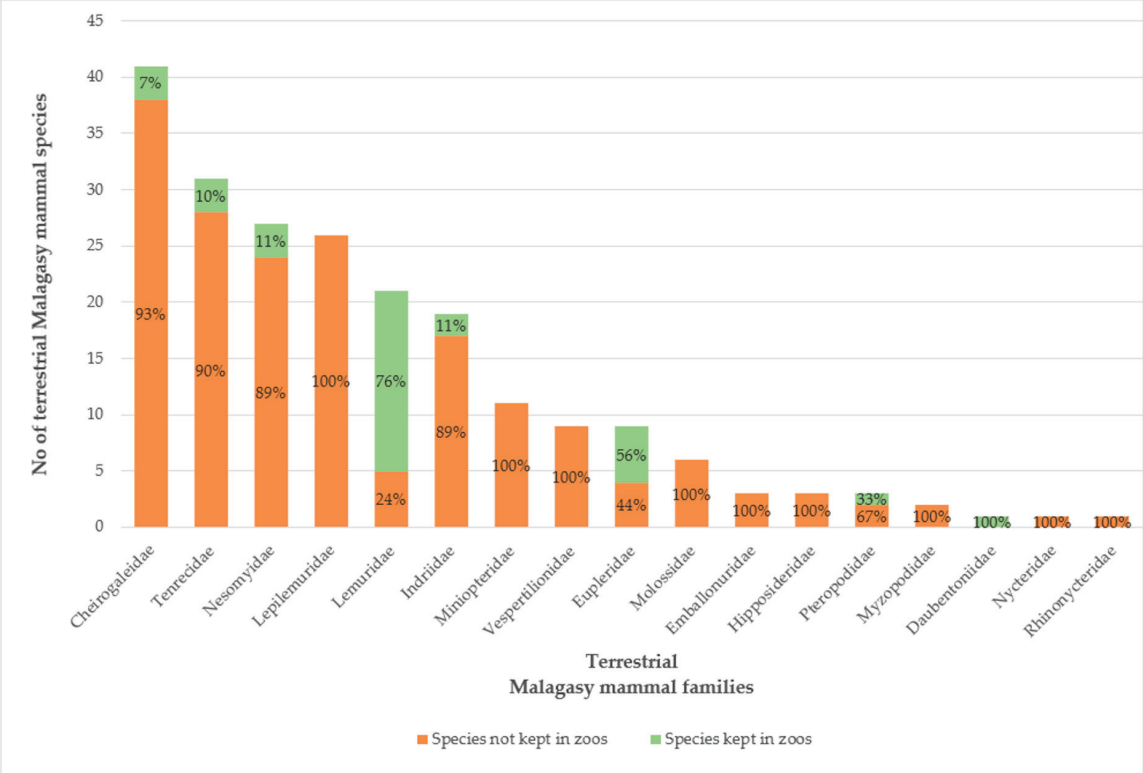

Figure 4. Percentage of terrestrial Malagasy species per family kept and not kept in zoos. Orange = percent of species per family not kept in zoos, Green = percent of species per family kept in zoos.

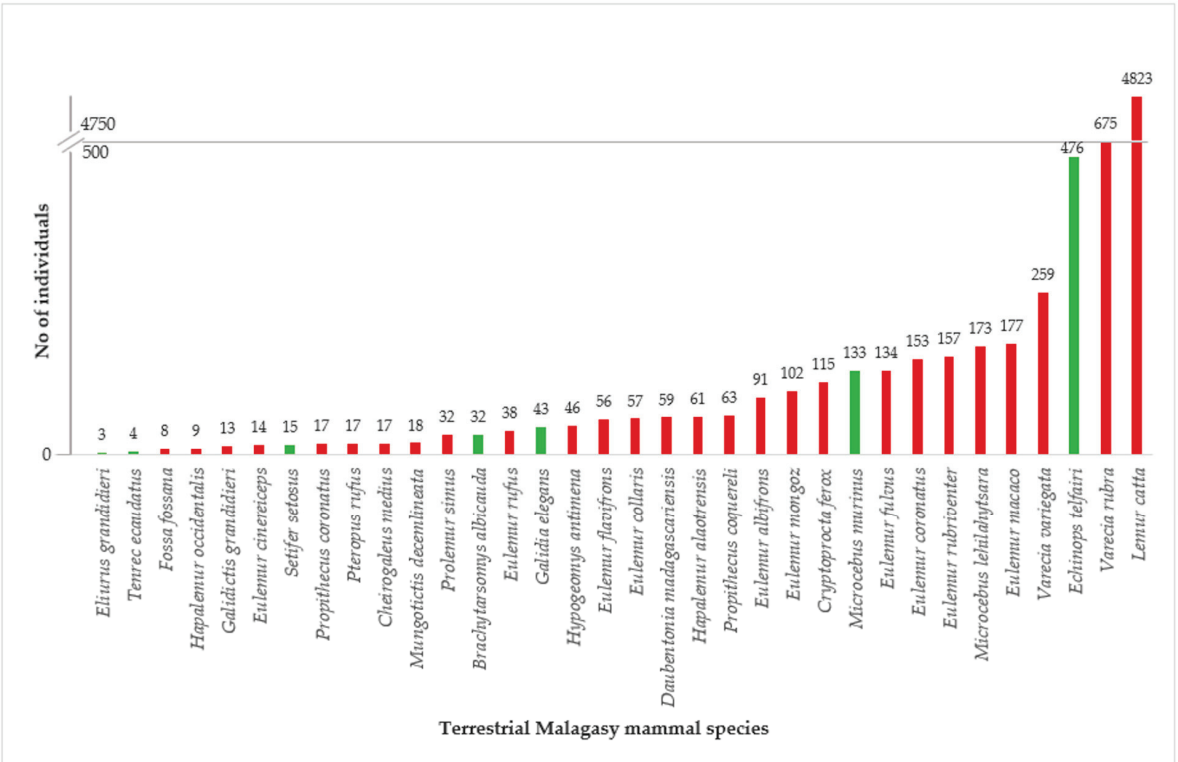

Figure 5. Population numbers of Malagasy mammal species registered in ZIMS (2024) [36] in zoological institutions worldwide. Red = threatened, Green = not threatened. Broken Y-axis between 500 and 4750 individuals.

The most represented family in zoos was Lemuridae, of which 76% (N = 16) of all 21 species were kept in zoos. This family also comprises the threatened species *Lemur catta*, which had the highest number of individuals (N = 4823), followed by *Varecia rubra* (N = 675) and *V. variegata* (N = 259). The family Eupleridae was the second most representative in zoos, with 56% (N = 5). The family Cheirogaleidae was the most diverse, including 40 species, of which only 8% (N = 3) were in zoos, followed by the family Tenrecidae, with 31 species, of which 10% (N = 3) were kept in zoos. The Tenrec *Echinops telfairi* was the non-threatened species with the largest ex situ population, with 476 individuals. The families Nesomyidae and Indriidae each had 11% of species per family (N = 3 and N = 2, respectively) in ex situ populations. The Critically Endangered Aye-aye (*Daubentonia madagascariensis*), which is the only species of the family Daubentoniidae, was represented by 56 individuals in zoos (Figures 4 and 5).

Wild lemurs' minimal viable population size is approximately 40 adult individuals [45]. Of 34 terrestrial Malagasy mammal species that were held, 13 species had less than 40 individuals distributed globally in zoos, including *Fossa fossana* (N = 8) and *Hapalemur occidentalis* (N = 9) with the least number of individuals. In total, 1545 institutions reported the keeping of terrestrial Malagasy mammal species, with the possibility of multiple counts, as not every zoo exclusively kept a single species. With 1335 of the 1545, the majority of the institutions held threatened species. With 953 institutions, Europe had the most institutions that held terrestrial Malagasy mammal species, followed by North America with 420, Asia with 111, Australia with 23, Africa with 18, and South America with 9 zoological institutions. A similar trend emerged with the number of species held on each continent, as Europe held all 34 terrestrial Malagasy mammal species that are kept worldwide in zoos, followed again by North America with 22, Asia with 13, Africa with 9, and South America with 3 species. The only terrestrial mammal species of Madagascar kept in zoos on the Australian continent was *Lemur catta*.

According to ZIMS and ZTL, the families Lepilemuridae, Miniopteridae, Vespertilioinidae, Molossidae, Emballonuridae, Hipposideridae, Myzopodidae, Nyteridae, and Rhinonycteridae were not represented in zoos (Figure 4). The analysis showed that another 26 terrestrial Malagasy mammal species were held in zoological institutions in the past, among them the Critically Endangered species *Hapalemur aureus*, *Indri indri*, *Lepi-lemur ruficaudatus*, *Propithecus diadema*, *Propithecus tattersalli*, and *Propithecus verreauxi*.

Based on the ZIMS database, 28 of the 34 terrestrial Malagasy mammal species in zoos reproduced successfully in the last 12 months. Of the 28 species with successful reproduction in zoos, 23 were threatened, including the 5 microendemic species *Hapalemur alaotrensis* with 6, *Eulemur flavifrons* with 7, *Hypogeomys antimena* with 8, *Propithecus coronatus* with 3, and *Propithecus coquereli* with 12 offspring in the last 12 months. In total, 233 breeding institutions were documented in ZIMS with several possible listings, as zoos might breed more than one species. The percentage of the 34 terrestrial mammal species of Madagascar kept in zoos that participated in breeding programs was 62% (N = 21), of which 6 species were included in the EEP, 5 in the SSP, and 10 species in both breeding programs. Furthermore, two species were recorded in the ESB.

The sex ratio of the 34 terrestrial Malagasy mammal species held in zoos was relatively proportional, with 45% females and 55% males (±12.55%). In general, the number of single-sex male individuals (N = 1039) kept in zoos was higher than those of females (N = 383).

Of all terrestrial Malagasy mammal species kept in zoos, 18% (N = 6) (Figure 6) were microendemics, which was only 8% of all microendemic mammal species of Madagascar. Furthermore, 23% (N = 9) of regional endemic terrestrial Malagasy mammals and 20% (N = 19) of the total amount of endemic mammal species of Madagascar were represented in zoos.

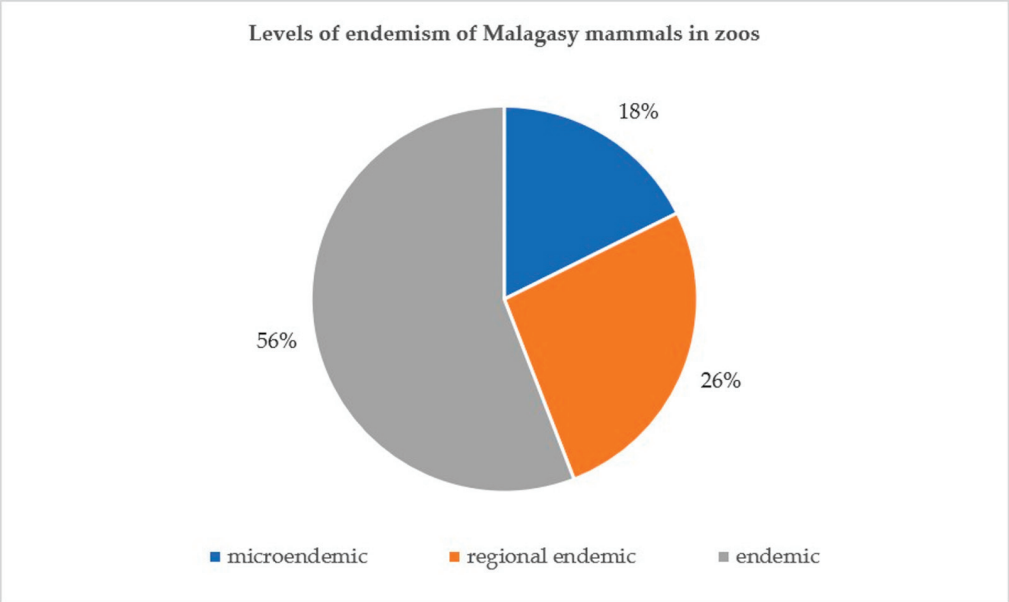

Figure 6. Distribution of endemism levels of terrestrial Malagasy mammals in zoos.

3.4. CITES

According to CITES, 53% (N = 106) of the terrestrial Malagasy mammal species are listed under Appendix I, and 22 of the 106 species were held in zoos. Another 2% (N = 4) of Madagascar´s terrestrial mammal species are documented under Appendix II, of which 3 were kept in zoos. With 48% (102), nearly half of terrestrial Malagasy mammal species are not listed under CITES; however, 9 of the 102 species were held in zoological facilities. Additionally, 101 of the 106 terrestrial mammal species of Madagascar that were listed under Appendix I were also listed as threatened by the IUCN. Of the 102 terrestrial Malagasy mammal species that were not listed under CITES, 22 were threatened species, according to IUCN.

3.5. EDGE of Existence Programme

Based on the EDGE of Existence Programme, 84 (40%) of the 212 terrestrial Malagasy mammal species had an EDGE score. *Daubentonia madagascariensis* had the highest EDGE score of 20.13 and was ranked in the second place of all mammal species worldwide on the EDGE list. Three other terrestrial mammal species of Madagascar had an EDGE score over ten, namely *Varecia rubra* (11.31), *Varecia variegata* (11.29), and *Indri indri* (10.44). *Eulemur rufus* had the lowest EDGE score of Malagasy mammals, with 3.55. Of the 84 terrestrial Malagasy mammal species ranked on the EDGE list, 23 were kept in zoos.

3.6. Prioritization

The results presented in Table 1 show the top 10 of all 212 terrestrial Malagasy mammal species that need priority conservation attention. All ten species are microendemic, Critically Endangered according to the IUCN, and have an EDGE score of $\leq$4.45. With six species, the family Indriidae has the highest number of species in the prioritization list, followed by Cheirogaleidae with two species. The families Lepilemuridae and Lemuridae each have one species included in the list. All families in the top ten priority list belong to the lemur order (Table 1). A comprehensive overview of prioritization within each Malagasy mammal family is provided in Appendix B.

Table 1. Top ten priority species of terrestrial Malagasy mammals.

Species	Family	Endemism Level	IUCN Status	EDGE Score
Hapalemur aureus	Lemuridae	microendemic	CR	5.41
Propithecus tattersalli	Indriidae	microendemic	CR	5.31
Propithecus candidus	Indriidae	microendemic	CR	5.25
Propithecus perrieri	Indriidae	microendemic	CR	5.21
Microcebus gerpi	Cheirogaleidae	microendemic	CR	5.14
Lepilemur septentrionalis	Lepilemuridae	microendemic	CR	4.96
Avahi cleesei	Indriidae	microendemic	CR	4.63
Avahi unicolor	Indriidae	microendemic	CR	4.63
Propithecus deckenii	Indriidae	microendemic	CR	4.50
Microcebus berthae	Cheirogaleidae	microendemic	CR	4.45

3.7. Protected Area and Key Biodiversity Area Coverage

Both species richness of Malagasy mammal species and species richness of threatened Malagasy mammal species are high in PAs. High values in endemism occur both outside and inside PAs. The numbers of species and numbers of threatened Malagasy mammal species differ between the PAs in Madagascar and are highest in the east of the country with its subhumid and lowland forests.

Of the 212 terrestrial Malagasy mammal species, 8% (N = 17) are not covered by PAs, of which 13 species are threatened with extinction. Furthermore, *Propithecus perrieri* and *Lepilemur septentrionalis* are listed in the top ten priority list (Table 1) and show no coverage by PAs. Most of the terrestrial Malagasy mammals´ habitats, with 96% (N = 203), are located within key biodiversity areas. The results show regions in Madagascar with a high number of mammal species occurring in KBAs that are not included in protected areas (Figure 7).

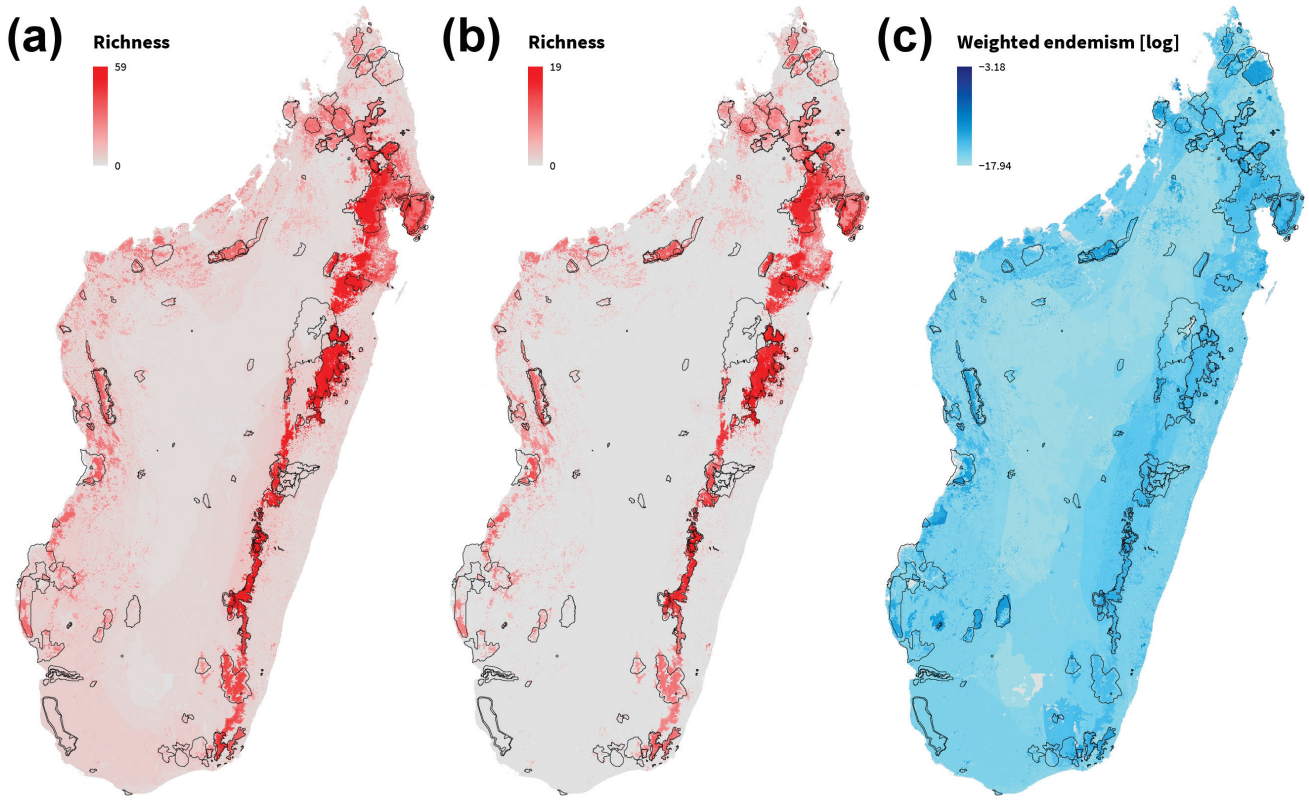

Figure 7. *Cont.*

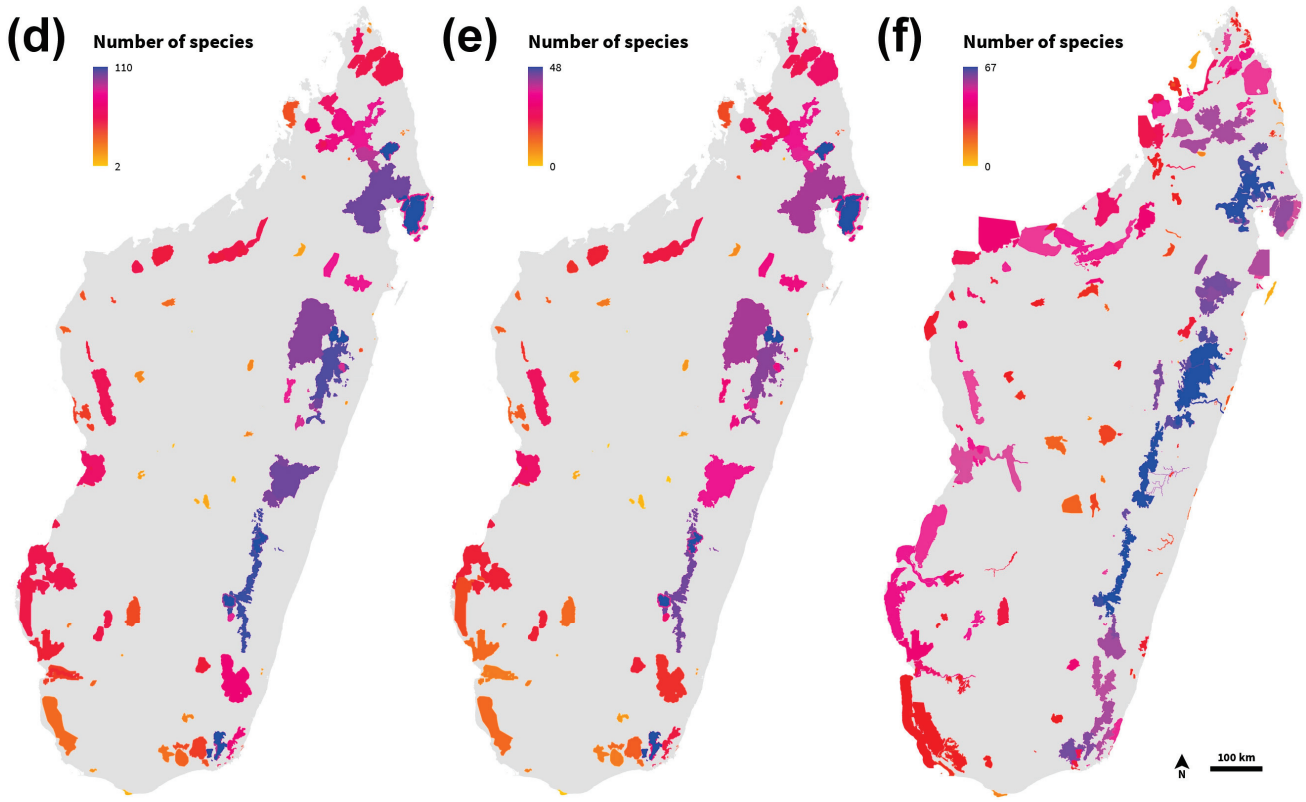

Figure 7. Spatial patterns of species richness, endemism, protected area coverage, and key biodiversity area coverage of terrestrial mammal species in Madagascar. (**a**) Richness of all species, (**b**) richness of threatened species, (**c**) weighted endemism, (**d**) number of species per PA, (**e**) number of threatened species per PA, (**f**) number of species per KBA. Darker colors indicate higher values. PAs are outlined in black.

4. Discussion

In total, 98% of the 212 terrestrial mammal species in Madagascar are endemic and, therefore, occur nowhere else in the world, making Madagascar one of the most important mammalian diversity hotspots in the world [46]. Our findings reveal that among the 208 endemic species, 38 are regional endemics, while 82 are microendemics. Since there are various categories of endemism and no universally recognized method to measure endemism levels [47], the number of microendemics and regional endemics among terrestrial Malagasy mammal species may be even higher, depending on the concept applied. The discovery of many cryptic *Microcebus* species over the past decades [13], along with recent molecular studies of the bat genera *Hipposideros* [48] and *Miniopterus* [49], further suggest an increasing number of terrestrial Malagasy mammal species. Given the heightened risk of extinction for undiscovered mammal species [31], the continuous deforestation in Madagascar [23], and the vast area of endemism centers throughout the country [34], on-site conservation should be one of the substantial pillars of conserving terrestrial mammal species in Madagascar. Since a high number of terrestrial Malagasy mammal species was documented for subhumid forests (N = 149), lowland forests (N = 134), and dry deciduous forests (N = 113), in situ mammal conservation should be emphasized in these ecoregions. Mangroves are the ecoregion with the least amount of terrestrial Malagasy mammal species, which could be due to the ecoregion´s small overall area.

Only 53% of the terrestrial Malagasy mammal species are listed under CITES Appendix I and are, therefore, banned from international commercial trading. Overexploitation and illegal wildlife trade are two of the biggest threats to biodiversity [23]. More significant than international trade, despite nationwide prohibition, is bushmeat hunting. This practice is widely used across the country, especially in rural and poor regions, to ensure food

security [50]. Bushmeat hunting and related national trade remain a major concern for Malagasy mammals, particularly for lemur species [51].

Our research showed that 60% (N = 127) of terrestrial Malagasy mammal species are threatened with extinction. For the 13 species that are classified by the IUCN as Data Deficient, further research is required in order to assign another Red List category since 64% of Data Deficient terrestrial mammal species are predicted to have a risk of extinction [52]. Despite the growing number of Madagascar´s national parks and reserves, habitat destruction persists outside and inside protected areas [53]. Furthermore, the ongoing deforestation in Madagascar poses a threat of inbreeding due to habitat fragmentation, especially in humid forests [23]. Consequently, the survival of terrestrial mammal species of Madagascar cannot only rely on in situ conservation. Ex situ efforts in zoological institutions have to be increased for the conservation of threatened Malagasy mammal species and the effective implementation of the One Plan Approach, viz. to save species from extinction and to buy time, when conservation measures on site cannot be conducted in time.

This analysis does not consider terrestrial Malagasy mammal species that are held in private ownership or other institutions such as universities or museums. Additionally, data entries in the ZIMS or ZTL database may change on a regular basis, and zoological institutions are not obligated to transmit or update their information. However, based on our sources, only 16% of terrestrial mammal species of Madagascar are in ex situ populations, of which 74% are threatened under IUCN. Over half of the terrestrial Malagasy mammal species in zoos are lemur species (Appendix A). Possible reasons for this overrepresentation could be their popularity among visitors [54], given that some lemur species are present in numerous zoos worldwide (e.g., *Lemur catta*, *Varecia rubra*, *Varecia variegata*). These species are mainly diurnal and have noticeable color patterns and a relatively large body size, making it easy for visitors to see them [54]. Here, zoo facilities could be better used in the sense of the One Plan Approach, viz. acting as a modern ark. Species that are nocturnal and small could be emphasized for the public through special display and awareness of their uniqueness, e.g., the Aye-aye with its characteristic appearance that is the only representative of the family Daubentoniidae.

Out of the nine families of terrestrial Malagasy mammal species that are not represented in zoos, eight belong to chiropteran families, including Myzopodidae, which is the only bat family endemic to the island [55]. Furthermore, the endemic lemur family Lepilemuridae has no representation in zoological facilities but encompasses 25 species that are all threatened with extinction [19]. Two of the species were kept in the past (*L. ruficaudatus*, *L. mustelinus*); however, no kept individual has been reported for the last 30 years (Figure 4, Appendix A Table A1).

Given the biodiversity crises and the limited time, budget, and resources for conserving threatened species, the discussion on prioritizing species to ensure their survival is not new [56]. The EDGE of Existence program ranks species according to their evolutionary distinctiveness and threat status [39]. We found that 60% of terrestrial Malagasy mammal species had no allocated EDGE Score; furthermore, 43 species are threatened with extinction (Appendix B). Due to the overall high endemism level in mammalian species of Madagascar [12], we distinguished between three endemism levels to further prioritize species. Since microendemics only occur in restricted areas, their risk of extinction is highest, particularly for those already assigned a threatened status. Thus, zoological institutions, especially those with limited financial or spacious capacity, should focus on keeping and breeding priority species as our list proposes.

According to our prioritization list, special conservation attention should be focused on terrestrial Malagasy mammal species that are not kept in zoos, are microendemic, have a high risk of extinction, and have a high EDGE score. The top ten priority species can be found in Table 1. Furthermore, species within each Malagasy mammal family were also prioritized. One of the families with the highest overall priority score is Indriidae. Given their slow reproduction rate, particularly in comparison with other lemurs and primates [57] and, therefore, their higher risk of extinction [58], establishing ex situ populations could

buy time for threatened wild populations [6]. Another family with a high prioritization is Cheirogaleidae, primarily species of the genus *Microcebus* with restricted geographic ranges [59]. A focus should also be drawn to the lemur family Lepilemuridae as 88% of its species are microendemic, all species are threatened according to the IUCN, and none are currently kept in zoos. The main limitation of the prioritization list was the missing data on the EDGE score of more than half of the terrestrial Malagasy mammal species (Appendix B Table A2).

Of the 34 terrestrial Malagasy mammal species held in zoos, 13 species include less than 40 individuals (Appendix A Table A1). As the minimal viable population size for lemurs in the wild is considered to be around 40 adult individuals [45], it is vital to increase the number of individuals of these species in ex situ populations, especially for threatened and microendemic species with a declining population such as *Propithecus coronatus*.

To ensure the suitability and effectiveness of the establishment of ex situ populations, a considered management plan is necessary, as proposed in the IUCN guidelines on ex situ management for conservation. This tool supports the decision-making process on crucial steps such as the evaluation of risks, the acquisition of resources, and the attributes of the ex situ population. Well-managed ex situ populations can ultimately help to prevent the extinction of wild populations and secure their long-term survival [60].

For a more prioritized keeping and breeding program to take place, zoos should consider reducing the number of individuals of non-threatened terrestrial Malagasy mammal species with a high number of individuals held, such as *Echinops telfairi* with 476 specimens or even the threatened species *Lemur catta* with currently 4823 specimens worldwide (Appendix A Table A1). This way, zoos could reallocate their resources towards ensuring 'insurance populations' [6] for highly threatened and prioritized terrestrial mammal species of Madagascar that have small or no ex situ populations.

The majority of terrestrial Malagasy mammal species in zoos (62%) are in breeding programs. The reproductive success in the last 12 months of these species was 100%. On the contrary, all terrestrial mammal species of Madagascar in zoos that did not have successful reproductions in the last 12 months are simultaneously not registered in breeding initiatives, according to ZIMS (Appendix A Table A1). This highlights the importance of the maintenance of studbooks, the exchange of individuals, and the research and monitoring of reproductive individuals. Currently, the main focus on kept terrestrial Malagasy mammals lies in Europe and North America, with only a few zoological institutions keeping species in Africa and Oceania. For more diverse breeding programs and for establishing secure ex situ populations, an overall expansion of conservation breeding networks is needed.

Zoos also play a crucial role in filling the data gap for terrestrial Malagasy mammal species that lack life history information to allow for better keeping and breeding success. One prominent example is the review of the crowned sifaka (*Propithecus coronatus*) that draws from 25 years of captive management experience in an EEP [61]. In North America, the Duke Lemur Center provides life history data of 19 lemur species throughout its 50 years of existence, being involved in multiple SSPs while also supporting in situ conservation in Madagascar [62].

For many species, it makes sense to have a broader distribution of ex situ populations worldwide. That helps to minimize the risk of losing animals through diseases kept only at one institution. One example is *Propithecus coquereli*. This species was mainly managed at the Duke Lemur Center and other zoos in the US. Recently, we have established a population in Europe. Zoos in Berlin, Chester, and Cologne participate in the European Studbook, which is run by Tierpark Berlin. For this and many other species, we need to expand our ex situ management to be more effective. Additionally, more holders lead to more experience in the captivity of the managed species, which again improves the ex situ efforts.

Despite the growing number of protected areas in Madagascar [23], not all terrestrial Malagasy mammal species can be effectively protected within these areas. Global analysis shows that an average of 14% of threatened mammals and their habitat are not covered by

PAs [63,64]. Our results reveal that only 8% of terrestrial Malagasy mammal species are not found in PAs, yet most of these species are threatened with extinction. Especially terrestrial mammal species in Madagascar that do not benefit from PA coverage can be supported by ex situ populations.

The majority of terrestrial Malagasy mammal species (96%) occur within key biodiversity areas. However, we also found regions, e.g., along the west coast (Figure 7), that are KBAs with a high number of mammal species but without protected area coverage. For the further expansion of Madagascar's protected area network, these sites should be prioritized.

It must be acknowledged that range estimates and preferred habitat assessments currently listed by IUCN are based on expert opinion and, hence, represent current knowledge. Both may be refined and updated as soon as new information becomes available. This may introduce some uncertainty in our analyses as especially rare and poorly understood species may either occupy habitat types currently not listed by IUCN or occur beyond their currently assumed extent of occurrence or area of occupancy as indicated by the IUCN range polygons.

Several conservation and breeding centers are located in Madagascar such as the Parc Botanique et Zoologique de Tsimbazaza in Antananarivo or the Ivoloina Parc Zoologique in Toamasina [65]. To ensure the survival of terrestrial Malagasy mammal species and to promote healthy and genetically diverse populations as the OPA advocates [4], it is vital to support existing ex situ conversation programs in Madagascar. These facilities can furthermore contribute to educational and research purposes and facilitate the reintroduction of terrestrial Malagasy mammal species born in human care [65].

The prioritization list does not consider species that have a low prioritization but are easily kept and bred with minimal effort and resources or show similarities with species that have been held successfully. The tenrec species *Geogale aurita* presents potential for keeping due to its comparable life history traits with *Echinops telfairi*, a species widely held in zoological collections globally. Both tenrec species are nocturnal, inhabit dry deciduous forests, and are insectivores [57].

Given the persistent threat of habitat loss and hunting [23], low-priority species could become endangered in the near future. From a global view, prominent examples of the past are the passenger pigeon (*Ectopistes migratorius*), which went extinct within a few decades despite high abundances [66], and the long-tailed macaque (*Macaca fascicularis*), whose IUCN threat status increased from Least Concern to Endangered in less than 15 years [67]. These cases illustrate that the persistent monitoring of now low-priority species is needed to ensure fast conservation actions.

In order to conserve the unique terrestrial mammal diversity of Madagascar, improving and expanding in situ measures as well as effective ex situ conservation planning are required. Through this study, we aim to provide a guideline for zoos to prioritize ex situ conservation for threatened terrestrial Malagasy mammal species.

5. Recommendations

Based on our findings, we recommend prioritizing threatened Malagasy mammal species for collaborative conservation breeding programs according to the provided list. The prioritization process should involve the following considerations.

1. Include overlooked threatened taxa into breeding programs, such as small-bodied and nocturnal species, e.g., Nesomyidae, *Cheirogaleus* spp., *Lepilemur* spp. This is easiest for threatened species where historic expertise exists (e.g., *Mirza coquereli*, *Phaner furcifer*) or where similar, often closely related, less threatened species are kept in zoos but could be exchanged with their threatened counterparts (e.g., *Echinops telfairi* with threatened members of Tenrecidae).

2. Aim to increase the number of individuals for threatened species that are prioritized for breeding but currently kept in very small populations. Examples are *Prolemur simus*, *Eulemur mongoz*, and many other lemur species.
3. Reduce the number of non-threatened species or the number of individuals of commonly kept threatened species. Examples of the latter are *Lemur catta* and *Varecia rubra*.

In order to achieve this successfully, conservation breeding networks should be expanded to different locations, including in-country conservation breeding programs. Following the One Plan Approach, breeding programs should connect and cooperate with existing on-site conservation programs in Madagascar. Finally, zoological institutions should highlight species of conservation value that are inconspicuous because of their appearance or lifestyle and, thus, easily overlooked by story-telling to raise conservation awareness for visitors.

6. Conclusions

The findings of our study highlight the critical need for integrating in situ and ex situ conservation initiatives for terrestrial Malagasy mammal species following the One Plan Approach. While protected areas play a crucial role in safeguarding habitats, complementary efforts within zoological institutions are vital for the survival of threatened terrestrial mammal species of Madagascar. Our study proposes a prioritization framework to guide ex situ conservation efforts, emphasizing the importance of focusing resources on species most at risk of extinction. Successful ex situ measures require strategic management of populations in human hands, including the reallocation of resources from abundant or non-threatened terrestrial Malagasy mammal species to those of a higher prioritization, such as highly threatened microendemic species. Moreover, collaborative breeding programs and data sharing among institutions are essential for maximizing reproductive success and genetic diversity to ensure the long-term survival of Madagascar's terrestrial mammal species.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Terrestrial Malagasy mammals currently or formerly kept in zoological institutions. Threat status and population trend according to the IUCN Red List of Threatened Species (2023). DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered. ↓ = decreasing, ↑ = increasing, – = stable, ? = unknown. Tot. Ind. = total number of individuals kept, Tot. M = total number of males kept, Tot. F = total number of females kept, Tot. O = total number of individuals without determined sex, Tot. Inst = total number of zoological institutions keeping individuals, No. of Births = number of births in the past 12 months, Tot. Breeding Inst. = total number of breeding institutions, EEP = European Endangered Species Program, ESB = European Studbook, SSP = Species Survival Plan, ZIMS = Zoological Information Management Software, ZTL = Zootierliste, CITES = Appendices listing.

Family *Species*	Threat Status	Population Trend	Tot. Ind.	Tot.M	Tot.F	Tot. O	Tot. Inst.	No. of Births	Tot. Breeding Inst.	EEP/ ESB/ SSP	Species Kept	From (year)	Until (year)	ZIMS/ ZTL	EDGE	EDGE Rank	CITES
Cheirogaleoidae																	
Allocebus trichotis	EN	↓									past	1991	2002	ZIMS	4.31	307	I
Cheirogaleus crossleyi	VU	↓									past	1967	1971	ZIMS			I
Cheirogaleus major	VU	↓									past	1978	1993	ZIMS			I
Cheirogaleus medius	VU	↓	17	5	2	10	1	3	1		today	1965		ZIMS			I
Microcebus lehilahytsara	NT	↓	173	89	83	1	7	28	2	EEP	today	2005		ZIMS	3.75	452	I
Microcebus murinus	LC	↓	133	65	65	3	28	21	4	EEP/SSP	today	1967		ZIMS			I
Microcebus myoxinus	VU	↓									past	1910	1911	ZIMS	3.7	471	I
Microcebus rufus	VU	↓									past	1973	2005	ZIMS	3.79	441	I
Mirza coquereli	EN	↓									past	1986	2012	ZIMS	5.11	101	I
Mirza zaza	VU	↓									past	1982	2012	ZIMS			I
Phaner furcifer	EN	↓									past	1986	1996	ZIMS	4.01	394	I
Daubentoniidae																	I
Daubentonia madagascariensis	EN	↓	59	28	29	2	15	4	4	EEP/SSP	today	1862		ZIMS	20.13	2	I

Table A1. *Cont.*

Family *Species*	Threat Status	Population Trend	Tot. Ind.	Tot.M	Tot.F	Tot. O	Tot. Inst.	No. of Births	Tot. Breeding Inst.	EEP/ ESB/ SSP	Species Kept	From (year)	Until (year)	ZIMS/ ZTL	EDGE	EDGE Rank	CITES
Eupleridae																	
Cryptoprocta ferox	VU	↓	115	64	51	0	55	13	4	EEP/SSP	today	1954		ZIMS	4.93	143	II
Fossa fossana	VU	↓	8	6	2	0	3	2	2		today	1966		ZIMS	4.61	198	II
Galidia elegans	LC	↓	43	20	20	3	13	8	4	ESB	today	1966		ZIMS			
Galidictis fasciata	VU	↓									past	1905	1963	ZTL	4.2	366	
Galidictis grandidieri	EN	↓	13	8	5	0	4	0	0		today	2017		ZIMS	4.89	149	
Mungotictis decemlineata	EN	↓	18	7	11	0	9	1	1	ESB	today	1997		ZIMS	4.89	151	
Salanoia concolor	VU	↓									past	1902	1913	ZTL	4.22	364	
Indriidae																	
Indri indri	CR	↓									past	1965	1965	ZIMS	10.44	16	I
Propithecus coquereli	CR	↓	63	29	33	1	15	12	4	EEP/SSP	today	1962		ZIMS	4.52	218	I
Propithecus coronatus	CR	↓	17	12	5	0	6	3	3	EEP	today	1987		ZIMS	4.56	208	I
Propithecus diadema	CR	↓									past	1993	2012	ZIMS	5.23	72	I
Propithecus tattersalli	CR	↓									past	1987	2008	ZIMS	5.31	58	I
Propithecus verreauxi	CR	↓									past	1984	2002	ZIMS	4.50	225	I
Lemuridae																	
Eulemur albifrons	VU	↓	91	48	39	4	31	5	2	SSP	today	1969		ZIMS	4.23	354	I
Eulemur cinereiceps	CR	↓	14	7	7	0	5	0	0		today	2002		ZIMS			I
Eulemur collaris	EN	↓	57	30	26	1	21	3	3	SSP	today	1962		ZIMS	4.23	355	I
Eulemur coronatus	EN	↓	153	82	69	2	50	10	7	EEP/SSP	today	1955		ZIMS	4.42	265	I
Eulemur flavifrons	CR	↓	56	28	28	0	20	7	4	EEP/SSP	today	1985		ZIMS	5.00	124	I
Eulemur fulvus	VU	↓	134	71	60	3	45	3	3	SSP	today	1972		ZIMS			I

Table A1. *Cont.*

Family *Species*	Threat Status	Population Trend	Tot. Ind.	Tot.M	Tot.F	Tot. O	Tot. Inst.	No. of Births	Tot. Breeding Inst.	EEP/ ESB/ SSP	Species Kept	From (year)	Until (year)	ZIMS/ ZTL	EDGE	EDGE Rank	CITES
Eulemur macaco	EN	↓	177	89	87	1	67	16	13	EEP	today	1904		ZIMS	3.70	469	I
Eulemur mongoz	CR	↓	102	60	39	3	33	12	9	EEP/SSP	today	1898		ZIMS	5.07	110	I
Eulemur rubriventer	VU	↓	157	85	70	2	53	4	4	EEP	today	1925		ZIMS	3.68	478	I
Eulemur rufus	VU	↓	62	29	31	2	28	5	3	SSP	today	1963		ZIMS	3.55	551	I
Eulemur sanfordi	EN	↓									past	1969	2015	ZIMS	4.25	346	I
Hapalemur alaotrensis	CR	↓	61	34	24	3	16	6	3	EEP	today	1985		ZIMS	5.38	48	I
Hapalemur aureus	CR	↓									past	1988	1995	ZIMS	5.41	47	I
Hapalemur griseus	VU	↓									past	1962	2022	ZIMS	3.99	399	I
Hapalemur occidentalis	VU	↓	9	6	3	0	4	1	1		today	1991		ZIMS	3.99	401	I
Lemur catta	EN	↓	4823	2415	2023	385	555	369	113	EEP/SSP	today	1961		ZIMS	4.76	167	I
Prolemur simus	CR	↓	32	10	20	2	10	3	2	EEP	today	1987		ZIMS	5.33	54	I
Varecia rubra	CR	↓	675	358	307	10	191	32	15	EEP/SSP	today	1983		ZIMS	11.31	13	I
Varecia variegata	CR	↓	259	133	95	14	82	11	5	EEP/SSP	today	1989		ZIMS	11.29	14	I
Lepilemuridae																	
Lepilemur mustelinus	VU	↓									past	1969	1973	ZIMS			I
Lepilemur ruficaudatus	CR	↓									past	1986	1993	ZIMS			I
Nesomyidae																	
Brachytarsomys albicauda	LC	?	32	9	13	10	6	17	3		today	2018		ZIMS			
Eliurus grandidieri	LC	?	3	1	2	0	1	0	0		today	2008		ZIMS			
Eliurus myoxinus	LC	?									past	1967	1967	ZIMS			
Hypogeomys antimena	CR	?	46	21	23	2	15	8	5		today	1990		ZIMS	4.94	139	

Table A1. *Cont.*

Family *Species*	Threat Status	Population Trend	Tot. Ind.	Tot.M	Tot.F	Tot. O	Tot. Inst.	No. of Births	Tot. Breeding Inst.	EEP/ ESB/ SSP	Species Kept	From (year)	Until (year)	ZIMS/ ZTL	EDGE	EDGE Rank	CITES
Pteropodidae																	
Pteropus rufus	VU	↓	17	5	2	10	1	3	1		today	2020		ZIMS			II
Tenrecidae																	
Echinops telfairi	LC	–	476	198	187	91	143	42	9	SSP	today	1975		ZIMS			
Hemicentetes nigriceps	LC	?									past	1966	2022	ZIMS			
Hemicentetes semispinosus	LC	?									past	1965	2003	ZIMS			
Microgale dobsoni	LC	↓									past	1966	1970	ZIMS			
Microgale talazaci	LC	↓									past	1966	1978	ZIMS			
Microgale thomasi	LC	↓									past	1966	1969	ZIMS			
Setifer setosus	LC	–	15	6	4	5	8	0	0		today	1966		ZIMS			
Tenrec ecaudatus	LC	–	4	4	0	0	4	0	0		today	1900		ZIMS			

Appendix B

Table A2. Prioritization list of terrestrial Malagasy mammal species sorted by families. Threat status according to the IUCN Red List of Threatened Species (2023). DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

Family *Species*	Species Kept	Endemism	IUCN	EDGE Score
Cheirogaleidae				
Microcebus gerpi	no	microendemic	CR	5.14
Microcebus berthae	no	microendemic	CR	4.45
Microcebus manitatra	no	microendemic	CR	0.00
Microcebus mamiratra	no	microendemic	EN	5.14
Phaner parienti	no	microendemic	EN	4.73
Microcebus bongolavensis	no	microendemic	EN	4.45
Microcebus jollyae	no	microendemic	EN	4.45
Microcebus margotmarshae	no	microendemic	EN	4.45
Microcebus sambiranensis	no	microendemic	EN	4.45
Microcebus simmonsi	no	microendemic	EN	4.45
Cheirogaleus lavasoensis	no	microendemic	EN	0.00
Cheirogaleus thomasi	no	microendemic	EN	0.00
Microcebus ganzhorni	no	microendemic	EN	0.00
Microcebus jonahi	no	microendemic	EN	0.00
Microcebus tanosi	no	microendemic	EN	0.00
Cheirogaleus andysabini	no	microendemic	EN	0.00
Microcebus danfossi	no	microendemic	VU	4.45
Microcebus ravelobensis	no	microendemic	VU	4.45
Microcebus rufus	no	microendemic	VU	3.79
Microcebus myoxinus	no	microendemic	VU	3.70
Microcebus griseorufus	no	microendemic	LC	0.00
Cheirogaleus grovesi	no	microendemic	DD	0.00
Microcebus boraha	no	microendemic	DD	0.00
Cheirogaleus sibreei	no	regional endemic	CR	5.68
Phaner electromontis	no	regional endemic	EN	4.70
Allocebus trichotis	no	regional endemic	EN	4.31
Phaner furcifer	no	regional endemic	EN	4.01
Cheirogaleus shethi	no	regional endemic	EN	0.00
Microcebus tavaratra	no	regional endemic	VU	3.75
Cheirogaleus crossleyi	no	regional endemic	VU	0.00
Cheirogaleus major	no	regional endemic	VU	0.00
Microcebus marohita	no	endemic	CR	5.14
Mirza coquereli	no	endemic	EN	5.11
Phaner pallescens	no	endemic	EN	4.72
Microcebus macarthurii	no	endemic	EN	4.45

Table A2. *Cont.*

Family *Species*	Species Kept	Endemism	IUCN	EDGE Score
Microcebus arnholdi	no	endemic	VU	4.45
Mirza zaza	no	endemic	VU	0.00
Microcebus lehilahytsara	yes	regional endemic	NT	3.75
Cheirogaleus medius	yes	endemic	VU	0.00
Microcebus murinus	yes	endemic	LC	0.00
Daubentoniidae *Daubentonia madagascariensis*	yes	endemic	EN	20.13
Emballonuridae				
Paremballonura atrata	no	endemic	LC	0.00
Paremballonura tiavato	no	endemic	LC	0.00
Coleura kibomalandy	no	endemic	DD	0.00
Eupleridae *Salanoia concolor*	no	microendemic	VU	4.22
Eupleres major	no	endemic	EN	5.30
Eupleres goudotii	no	endemic	VU	4.61
Galidictis fasciata	no	endemic	VU	4.20
Galidictis grandidieri	yes	microendemic	EN	4.89
Mungotictis decemlineata	yes	regional endemic	EN	4.89
Cryptoprocta ferox	yes	endemic	VU	4.93
Fossa fossana	yes	endemic	VU	4.61
Galidia elegans	yes	endemic	LC	0.00
Hipposideridae *Paratriaenops auritus*	no	regional endemic	VU	4.08
Macronycteris commersoni	no	endemic	NT	0.00
Paratriaenops furcula	no	widespread	LC	0.00
Indriidae *Propithecus tattersalli*	no	microendemic	CR	5.31
Propithecus candidus	no	microendemic	CR	5.25
Propithecus perrieri	no	microendemic	CR	5.21
Avahi cleesei	no	microendemic	CR	4.63
Avahi unicolor	no	microendemic	CR	4.63
Propithecus deckenii	no	microendemic	CR	4.50
Avahi betsileo	no	microendemic	EN	4.63
Avahi mooreorum	no	microendemic	EN	4.63
Propithecus edwardsi	no	microendemic	EN	4.54
Avahi occidentalis	no	microendemic	VU	4.60
Avahi peyrierasi	no	microendemic	VU	3.94
Indri Indri	no	regional endemic	CR	10.44
Propithecus diadema	no	regional endemic	CR	5.23
Propithecus verreauxi	no	regional endemic	CR	4.50

Table A2. *Cont.*

Family *Species*	Species Kept	Endemism	IUCN	EDGE Score
Avahi meridionalis	no	regional endemic	EN	4.63
Avahi ramanantsoavanai	no	regional endemic	VU	3.94
Avahi laniger	no	endemic	VU	3.94
Propithecus coronatus	yes	microendemic	CR	4.56
Propithecus coquereli	yes	microendemic	CR	4.52
Lemuridae				
Hapalemur aureus	no	microendemic	CR	5.41
Eulemur sanfordi	no	regional endemic	EN	4.25
Hapalemur meridionalis	no	endemic	VU	4.01
Hapalemur griseus	no	endemic	VU	3.99
Eulemur rufifrons	no	endemic	VU	0.00
Hapalemur alaotrensis	yes	microendemic	CR	5.38
Eulemur flavifrons	yes	microendemic	CR	5.00
Varecia rubra	yes	regional endemic	CR	11.31
Prolemur simus	yes	regional endemic	CR	5.33
Eulemur mongoz	yes	regional endemic	CR	5.07
Eulemur coronatus	yes	regional endemic	EN	4.42
Eulemur collaris	yes	regional endemic	EN	4.23
Eulemur macaco	yes	regional endemic	EN	3.70
Eulemur rufus	yes	regional endemic	VU	3.55
Varecia variegata	yes	endemic	CR	11.29
Eulemur cinereiceps	yes	endemic	CR	0.00
Lemur catta	yes	endemic	EN	4.76
Eulemur albifrons	yes	endemic	VU	4.23
Hapalemur occidentalis	yes	endemic	VU	3.99
Eulemur rubriventer	yes	endemic	VU	3.68
Eulemur fulvus	yes	endemic	VU	0.00
Lepilemuridae				
Lepilemur septentrionalis	no	microendemic	CR	4.96
Lepilemur ahmansoni	no	microendemic	CR	0.00
Lepilemur grewcockorum	no	microendemic	CR	0.00
Lepilemur hollandorum	no	microendemic	CR	0.00
Lepilemur jamesorum	no	microendemic	CR	0.00
Lepilemur ruficaudatus	no	microendemic	CR	0.00
Lepilemur sahamalaza	no	microendemic	CR	0.00
Lepilemur tymerlachsoni	no	microendemic	CR	0.00
Lepilemur aeeclis	no	microendemic	EN	0.00
Lepilemur betsileo	no	microendemic	EN	0.00
Lepilemur dorsalis	no	microendemic	EN	0.00

Table A2. *Cont.*

Family *Species*	Species Kept	Endemism	IUCN	EDGE Score
Lepilemur edwardsi	no	microendemic	EN	0.00
Lepilemur fleuretae	no	microendemic	EN	0.00
Lepilemur hubbardorum	no	microendemic	EN	0.00
Lepilemur leucopus	no	microendemic	EN	0.00
Lepilemur microdon	no	microendemic	EN	0.00
Lepilemur otto	no	microendemic	EN	0.00
Lepilemur petteri	no	microendemic	EN	0.00
Lepilemur randrianasoloi	no	microendemic	EN	0.00
Lepilemur scottorum	no	microendemic	EN	0.00
Lepilemur wrightae	no	microendemic	EN	0.00
Lepilemur mustelinus	no	microendemic	VU	0.00
Lepilemur ankaranensis	no	regional endemic	EN	4.25
Lepilemur milanoii	no	regional endemic	EN	0.00
Lepilemur seali	no	regional endemic	VU	0.00
Miniopteridae				
Miniopterus ambohitrensis	no	microendemic	LC	0.00
Miniopterus griffithsi	no	microendemic	DD	0.00
Miniopterus egeri	no	regional endemic	LC	0.00
Miniopterus mahafaliensis	no	regional endemic	LC	0.00
Miniopterus petersoni	no	regional endemic	DD	0.00
Miniopterus brachytragos	no	endemic	LC	0.00
Miniopterus gleni	no	endemic	LC	0.00
Miniopterus majori	no	endemic	LC	0.00
Miniopterus sororculus	no	endemic	LC	0.00
Miniopterus aelleni	no	widespread	LC	0.00
Miniopterus manavi	no	widespread	LC	0.00
Molossidae				
Mops atsinanana	no	endemic	LC	0.00
Mops jobimena	no	endemic	LC	0.00
Mops leucostigma	no	endemic	LC	0.00
Mormopterus jugularis	no	endemic	LC	0.00
Otomops madagascariensis	no	endemic	LC	0.00
Mops leucogaster	no	widespread	LC	0.00
Myzopodidae				
Myzopoda schliemanni	no	regional endemic	LC	0.00
Myzopoda aurita	no	endemic	LC	0.00
Nesomyidae				
Macrotarsomys ingens	no	microendemic	EN	4.76
Voalavo antsahabensis	no	microendemic	EN	4.69
Nesomys lambertoni	no	microendemic	EN	4.66

Table A2. *Cont.*

Family ***Species***	**Species Kept**	**Endemism**	**IUCN**	**EDGE Score**
Eliurus penicillatus	no	microendemic	EN	0.00
Eliurus petteri	no	microendemic	EN	0.00
Eliurus danieli	no	microendemic	LC	0.00
Eliurus antsingy	no	microendemic	DD	0.00
Eliurus ellermani	no	microendemic	DD	0.00
Macrotarsomys petteri	no	microendemic	DD	0.00
Eliurus carletoni	no	regional endemic	LC	0.00
Brachytarsomys villosa	no	endemic	VU	4.01
Brachyuromys betsileoensis	no	endemic	LC	0.00
Brachyuromys ramirohitra	no	endemic	LC	0.00
Eliurus majori	no	endemic	LC	0.00
Eliurus minor	no	endemic	LC	0.00
Eliurus myoxinus	no	endemic	LC	0.00
Eliurus tanala	no	endemic	LC	0.00
Eliurus webbi	no	endemic	LC	0.00
Gymnuromys roberti	no	endemic	LC	0.00
Macrotarsomys bastardi	no	endemic	LC	0.00
Monticolomys koopmani	no	endemic	LC	0.00
Nesomys audeberti	no	endemic	LC	0.00
Nesomys rufus	no	endemic	LC	0.00
Voalavo gymnocaudus	no	endemic	LC	0.00
Hypogeomys antimena	yes	microendemic	CR	4.94
Brachytarsomys albicauda	yes	endemic	LC	0.00
Eliurus grandidieri	yes	endemic	LC	0.00
Nycteridae *Nycteris madagascariensis*	no	endemic	DD	0.00
Pteropodidae *Eidolon dupreanum*	no	endemic	VU	0.00
Rousettus madagascariensis	no	endemic	VU	0.00
Pteropus rufus	yes	endemic	VU	0.00
Rhinonycteridae *Triaenops menamena*	no	endemic	LC	0.00
Tenrecidae *Microgale jenkinsae*	no	microendemic	EN	4.46
Microgale jobihely	no	microendemic	EN	4.46
Microgale monticola	no	microendemic	VU	3.77
Oryzorictes tetradactylus	no	microendemic	DD	0.00
Limnogale mergulus	no	regional endemic	VU	4.47
Microgale nasoloi	no	regional endemic	VU	3.77
Microgale dryas	no	regional endemic	VU	3.66

Table A2. *Cont.*

Family *Species*	Species Kept	Endemism	IUCN	EDGE Score
Hemicentetes nigriceps	no	regional endemic	LC	0.00
Microgale longicaudata	no	regional endemic	LC	0.00
Geogale aurita	no	endemic	LC	0.00
Hemicentetes semispinosus	no	endemic	LC	0.00
Microgale brevicaudata	no	endemic	LC	0.00
Microgale cowani	no	endemic	LC	0.00
Microgale dobsoni	no	endemic	LC	0.00
Microgale drouhardi	no	endemic	LC	0.00
Microgale fotsifotsy	no	endemic	LC	0.00
Microgale gracilis	no	endemic	LC	0.00
Microgale grandidieri	no	endemic	LC	0.00
Microgale gymnorhyncha	no	endemic	LC	0.00
Microgale majori	no	endemic	LC	0.00
Microgale parvula	no	endemic	LC	0.00
Microgale principula	no	endemic	LC	0.00
Microgale pusilla	no	endemic	LC	0.00
Microgale soricoides	no	endemic	LC	0.00
Microgale taiva	no	endemic	LC	0.00
Microgale talazaci	no	endemic	LC	0.00
Microgale thomasi	no	endemic	LC	0.00
Oryzorictes hova	no	endemic	LC	0.00
Echinops telfairi	yes	endemic	LC	0.00
Setifer setosus	yes	endemic	LC	0.00
Tenrec ecaudatus	yes	endemic	LC	0.00
Vespertilionidae				
Neoromicia malagasyensis	no	microendemic	VU	4.23
Hypsugo bemainty	no	microendemic	LC	0.00
Neoromicia robertsi	no	microendemic	DD	0.00
Neoromicia matroka	no	regional endemic	LC	0.00
Myotis goudoti	no	endemic	LC	0.00
Scotophilus marovaza	no	endemic	LC	0.00
Scotophilus robustus	no	endemic	LC	0.00
Pipistrellus raceyi	no	endemic	DD	0.00
Scotophilus tandrefana	no	endemic	DD	0.00

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