Research Topics

Biodiversity conservation and sustainable development of protected areas

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Biodiversity conservation and sustainable development of protected areas

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Editorial: Biodiversity conservation and sustainable development of protected areas

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Editorial on the Research Topic
Biodiversity conservation and sustainable development of protected areas

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The Kunming-Montreal Global Biodiversity Framework adopted during the 15th meeting of the Conference of the Parties (COP) to the Convention on Biological Diversity (CBD) in 2022, calls for the effective protection and management of 30% of the world's terrestrial, inland water, coastal and marine areas by the year 2030 (30×30 target). Protected areas (PAs) are the most direct and effective initiative to conserve biodiversity (Maxwell et al., 2020), while increasing evidence shows that the services provided by intact and functioning ecosystems in PAs are also of great value to human livelihoods, health, and well-being (Fischborn and Sandwith, 2021). With the consensus on sustainable development worldwide, the balance between nature conservation and poverty eradication has become an inevitable choice. Therefore, biodiversity conservation and sustainable development within and around PAs has become a central topic to the field of conservation ecology.

Recent studies on biodiversity conservation in PAs have focused on key ecosystems and rare and endangered species, and explored the status and changes of these conservation targets (Wang et al., 2022). The relationship between management inputs and biodiversity outcomes of PAs have also attracted researchers in different countries (Geldmann et al., 2018; Feng et al., 2022). Furthermore, the effectiveness of PAs is often influenced by regional development, and PAs may also have positive or negative impacts on regional social and economic development (den Braber et al., 2018; Naidoo et al., 2019). Thus, it is urgent to integrate conservation in the sustainable development of PAs and their surrounding regions, and to explore strategies for promoting a harmonious model of human-land interaction while maintaining or enhancing the effectiveness of conservation efforts within these areas.

Here, we proposed the Research Topic, "biodiversity conservation and sustainable development of protected areas" featured in the "Conservation and Restoration Ecology" section of Frontiers in Ecology and Evolution. This Research Topic aims to comprehensively explore the fundamental theories, technologies, approaches, and practices in the conservation of protected areas. Under this Research Topic, 11 articles have been successfully published with relevant findings, which provided useful insights.

a) The optimal spatial layout of PAs based on scientific methodology is an important issue in the establishment of PA system. That is, determining whether the location and scope of current PAs is reasonable, and making boundary and location adjustments are essential for effective conservation (He and Wei). Nogales et al. proposed a methodological framework for systematic conservation planning of freshwater ecosystems. He et al. explored an integrated optimization method applicable to PAs on islands.

b) The study on conservation status and effectiveness of PAs is to identify whether PAs can effectively protect the ecosystem and wildlife in the region (He and Wei). Shen et al. constructed an integrated framework through a series of assessments according to the state, trend, and relative change of each PA to explore the conservation effectiveness of PAs in the Three Parallel Rivers Region, China. Liu et al. found that climate and land-use changes would reduce the suitable habitats of Galliformes species in Southeast Asia and suggested establishing more PAs or adjusting the range of PAs based on the combined effect of climate and land-use changes. França et al. assessed the vulnerability to extinction of 55 snake species that occur in the Atlantic Forest of northeastern Brazil in Paraíba State, and found that only 18% of the snake fauna in this region is free of threats. They indicated that the fragmented habitats within some protected areas designated by the government were insufficient to support the survival of many animal populations, including snakes.

c) Exploring the relationship between conservation measures and changes of ecosystem in PAs is important to promote the effectiveness of PAs. Mndela et al. assessed the long-term impacts of shrub control on herbaceous vegetation and determined how wild ungulates modulate herbaceous vegetation response to shrub control. They suggested that the use of 50% shrub removal combined with wild ungulates is not only ecologically significant but also economically viable relative to 100% shrub removal. Zhang et al. studied the effects of rational clearcutting on the sprouting renewal of *Rhododendron* communities in one PA in Guizhou, China, and found that clearcutting improved the dominance of *Rhododendron* plants in the community and promoted sprouting renewal of *Rhododendron* populations. Another report used a molecular approach to investigate dietary flexibility of western red colobus (*Piliocolobus badius*) in two PAs with contrasting anthropogenic pressure (Aleixo-Pais et al.), with the aim to provide and implement sustainable and achievable conservation strategies within and around PAs.

d) The attitudes and perceptions of local communities are crucial for successful management of community-based conservation and sustainability of PAs. Xu et al. assessed the community perspectives of endangered species and the emotion and belief basis for participation in conservation in Sanjiangyuan National Park, China. They found that heterogeneity of preference was influenced by household income, religious beliefs, ethnicity, culture, and conservation awareness. Jones et al., analyzed the spatial distribution of perceived social impacts in 4 European Protected Areas and revealed that spatial proximity between local residents was the most important factors for predicting perceived impacts of PAs.

From these studies, we can conclude that the focus on conservation and management effectiveness of PAs has been a critical and welcomed step to achieve the 30×30 target. And how to take the most appropriate management measures, as well as how to keep the balance between biodiversity conservation and sustainable development of PAs and their surrounding regions, are crucial for enhancing the overall effectiveness of PAs. In conclusion, these studies promise to improve our knowledge of biodiversity conservation and sustainable development within and around PAs. We thank all authors who contributed to this Research Topic.

Author contributions

WW: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. TM: Writing – review & editing. IR: Writing – review & editing. WS: Writing – review & editing. BL: Writing – review & editing.

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Effects of clearcutting on species composition and community renewal of *Rhododendron* shrubs in northwest Guizhou Province, China

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Tree base sprouting is the main reproduction and expansion mode of *Rhododendron* plants. By leveraging the plot survey method, the species composition, community renewal, and species diversity in three *Rhododendron* shrub communities in control, and before and after clearcutting (CK, D_{3yr}, and D_{6yr}, respectively) were studied. Moreover, the dissimilarity of *Rhododendron* communities in CK, D_{3yr} and D_{6yr} were analyzed. The results showed that there were 26 plant species belonging to 14 families and 22 genera, in 3 communities in total, with 19 species of shrub plants and 7 species of herbaceous plants. The number of species increased from 13 in CK to 23 in D_{3yr} and then decreased to 20 in D_{6yr}. The height and coverage of D_{3yr} and D_{6yr} reached 39.3% and 58.9% of that of CK, respectively. The relative height of CK, D_{3yr}, and D_{6yr} was 43.79%, 65.4%, and 58.54%, respectively. The coverage of D_{3yr} and D_{6yr} reached 60.8% and 114.70% of that of CK, respectively. The relative coverage of CK, D_{3yr}, and D_{6yr} was 19.05%, 83.24%, and 77.32%, respectively. The important value of *Rhododendron* plants in the communities increased from 0.42 in CK to 0.74 in D_{3yr}, and then decreased to 0.67 in D_{6yr}. The α diversity in the shrub layer of D_{3yr} and D_{6yr} were generally lower than those of CK except Pielou evenness index. The β diversity indicates that the similarity between CK and D_{3yr} was lower, that between CK and D_{6yr} was moderate, and that between D_{3yr} and D_{6yr} was higher. The sprouting height and coverage of *Rhododendron* plants was significantly correlated with age and sprouting time. The sprouting ability of *Rhododendron* plants increased first and then decreased with age, while the sprouting ability of *Rhododendron* plants with age of 10–12 years was the strongest. Clearcutting measures can improve the dominance of *Rhododendron* plants in the communities, promote the sprouting and renewal of *Rhododendron* population, and accelerate the succession rate of communities.

KEYWORDS

***Rhododendron* shrub, clearcutting, species composition, species diversity, community renewal**

1 Introduction

Rhododendron is one of the largest genera of angiosperms with more than 1200 species worldwide, which have important ecological and socio-economic applications of ornamental, cultural, scientific, economic, and medicinal value (MacKay and Gardiner, 2017; Li et al., 2018; Ahmad et al., 2021). The genus is mostly distributed in subtropical evergreen broad-leaved mountain forests, mixed coniferous broad-leaved forests, coniferous forests, and dark coniferous forests at altitudes varying from 1000 to 3800 m (Fang and Min, 1995). It only forms a single species of *Rhododendron* shrub or *Rhododendron* dwarf forest in certain high mountains above the tree line (Sun, 2002). Guizhou Province is located at the edge of the distribution center of modern *Rhododendron* (Hengduan Mountain region in China) and its transition zone along the eastern distribution range (Dai et al., 2020). More than 110 species of *Rhododendron* plants are distributed naturally in Guizhou Province (Dai et al., 2020). Northwest Guizhou Province is a vital area for the distribution of *Rhododendron*, with six subgenera and more than fifty species accounting for approximately 50% of the total *Rhododendron* population in Guizhou. The Baili Rhododendron National Nature Reserve at the junction of Qianxi and Dafang counties is the most representative, with 43 species of *Rhododendron* plants (Wang et al., 2010; Chen et al., 2013). It is a typical representative of the largest and contiguously distributed natural wild *Rhododendron* communities in the world (Rong et al., 2009) which may play an important role in understanding *Rhododendron* shrub ecosystem processes, succession, and shrub management. However, both the quantity of seedlings and the renewal rate of *Rhododendron* plants are low (Yang et al., 2020a). Meanwhile, it is easy for *Rhododendron* plants to be replaced by highly competitive trees and other shrubs because of succession (Bian et al., 2006). Coupled with global changes in recent years, *Rhododendron* plants, particularly some narrowly distributed *Rhododendron* species, have begun to decline or even die (Ma et al., 2014; Liu et al., 2019; Yu et al., 2019; Bitayan et al., 2021).

Sprouting renewal primarily refers to dry base sprouting and underground stem sprouting (Lu et al., 2021). New plants are formed *via* dormant or adventitious buds from underground stems and stubble of trees to achieve forest renewal (Vesk and Westoby, 2004). Sprouting plants can use nutrients in the soil more effectively through their strong root system, which usually grows faster than seedlings and has stronger adaptability (Kauffman, 1991; Chen et al., 2019). Owing to the weak competitiveness and high canopy density of *Rhododendron* shrub communities in northwest Guizhou, seed renewal of the *Rhododendron* population is difficult, and tree-based sprouting renewal is the main mode of reproduction and expansion (Kong et al., 2019). At present, the primary measures to promote tree-based sprouting renewal are controlled forest fires, clearcutting and other natural disasters such as hurricane, mudslides (Li, 1992; Luoga et al., 2004; Subedi et al., 2019). However, forest fires are harmful as these reduce the sprouting ability of shrub communities (Tang et al., 2001). In contrast, planned clearcutting promotes the growth of shrub tillering branches, regenerates and rejuvenates plant clusters, and increases the canopy width and biomass (Shang et al., 2020). Following clearcutting, sprouting plants usually grow faster than seedlings (Vesk and Westoby, 2004).

Research on sprouting renewal of *Rhododendron* plants in global started late at present; further, research on sprouting and stress tolerance of wild *Rhododendron* plants is limited, decreasing the promotion and utilization of wild *Rhododendron* plants resources (MacKay and Gardiner, 2016). Although several studies have reported renewal of *Rhododendron* shrubs by disturbance, altitude, and climate changes (Singh et al., 2019; Choudhary et al., 2021; Jia et al., 2021), there is limited knowledge regarding the sprouting renewal of *Rhododendron* plants by clearcutting. In this study, the effects of rational clearcutting on the sprouting renewal of *Rhododendron* communities were studied to determine the effect of clearcutting–sprouting on the role of *Rhododendron* plants in *Rhododendron* shrub communities. The objectives were to (1) Can clearcutting promote the community renewal of *Rhododendron* shrubs? (2) Does age affect the response of *Rhododendron* shrubs to clearcutting? (3) Can the sprouting and regeneration of *Rhododendron* be predicted after clearcutting?

2 Material and methods

2.1 Overview of the study area

The study area is in the Tiaohuapo Scenic Spot in the Baili Rhododendron National Nature Reserve, Guizhou Province, China (27°23′22′′N and 105°51′52′′E), near the Jiaozi Mountain, at an altitude of 1700–1900 m. The climate of the region can be characterized as subtropical humid monsoon climate, with an annual average temperature and precipitation of 11.8°C, and 1150.4 mm, respectively, a frost-free period of 257 days, and an annual sunshine duration of 1335.5 h. Zonal vegetation is dominated by the evergreen broad-leaved mountain forest. The existing vegetation is primarily *Rhododendron* shrub species exhibiting succession and transitional characteristics (Li and Chen, 2005; Jiang et al., 2015). Among *Rhododendron* shrubs, *R. delavayi*, *R. annae*, and *Lyonia ovalifolia* are the main dominant species. The soil type is primarily yellow soil with an acidic pH (4.61–5.32).

2.2 Plot setting and survey

In August 2015, three 20 m × 20 m fixed quadrats were set in the study area to represent the control community (CK), and three 5 m × 5 m survey quadrats were set diagonally in each quadrat. The species, plant number, branch number, height, and canopy width of the shrubs as well as the species and number of the herbaceous plants in the quadrats were recorded. Each *Rhododendron* shrub in the fixed quadrat was labelled.

In conjunction with the guidelines of Management Office of the Baili Rhododendron National Nature Reserve, all plants in the fixed quadrat were deforested and recovered. The shrubs in the fixed quadrat were deforested in December 2015 and the stubble height was recorded as approximately 15 cm. The number of stubbles was also recorded. The age of shrubs was determined based on the rings of the main pile of shrubs. All other plants were deforested and eliminated.

The same method was used to survey and record the sprouting number, height, and canopy width of *Rhododendron* shrubs in August 2018 and August 2021. Moreover, the species number, height, and canopy width of other shrubs, as well as the species and number of herbaceous plants in the quadrats, were also surveyed. The communities surveyed in 2018 and 2021 were denoted as D_{3yr} (Community 3 years after clearcutting) and D_{6yr} (Community 6 years after clearcutting), respectively.

2.3 Data analyses

2.3.1 Importance value

IV of the shrub layer for plant species in the three annual communities (CK, D_{3yr}, and D_{6yr}) was calculated using the equation (Wang et al., 2023)

$$IV = (RH + RC + RD)/3 \tag{1}$$

where *RH* denotes the relative height, *RC* denotes the relative coverage, and *RD* denotes the relative density.

2.3.2 α-Diversity

The Margalef richness index (*R*), Simpson diversity index (*D*), Shannon–Wiener diversity index (*H*), and Pielou evenness index (*J*) were determined to measure the α-diversity of the three communities using the equations (Zhang et al., 2017)

$$R = (S - 1)/lnN \tag{2}$$

$$D = 1 - \sum_{i=1}^{S} P_i^2 \tag{3}$$

$$H = -\sum_{i=1}^{S} P_I \quad lnI \tag{4}$$

$$J = H/lnS \tag{5}$$

where P_i denotes the relative IV of the ith species, *S* denotes the number of species, and *N* denotes the number of individual plants in the quadrat.

2.3.3 β-Diversity

The Cody index (β_c), Whittaker index (β_{ws}), Jaccard index (C_j), and Sorenson index (C_s) were determined to measure the β-diversity of the three communities before and after clearcutting using the equations (Baselga, 2010)

$$\beta_c = [g(H) + L(H)]/2 \tag{6}$$

$$\beta_{ws} = ms/ma - 1 \tag{7}$$

$$Cj = j/(a + b - j) \tag{8}$$

$$Cs = 2j/(a + b) \tag{9}$$

where β_c and β_{ws} denote the dissimilarity measures, C_j and C_s denote the similarity measures, $g(H)$ denotes the number of species increased along the time gradient *H*, $L(H)$ denotes the number of plant species existing in the previous community but lost in the next community, *ms* denotes the total number of species recorded in the three communities, *ma* denotes the average number of species in each community, *a* denotes the number of species in community A, *b* denotes the number of species in community B, and *j* denotes the number of species shared by communities A and B.

2.3.4 Sprouting status

The ratio between the number of *Rhododendron* sprouts and stumps after clearcutting was determined to measure the ability of *Rhododendron* plant to rejuvenate and renew using the equation

$$RS = ES/NS \tag{10}$$

where *RS* denotes sprouting ability, *ES* denotes the number of sprouts, and *NS* denotes the number of stubbles.

2.4 Data processing and statistical analyses

SPSS 26.0 software was used to measure the correlation (*Pearson correlation*) and linear regression analysis between the height and coverage as well as clearcutting time and age of *Rhododendron*. Analysis of variance was performed ($p < 0.05$ indicates significant differences) to determine the difference in IV of community species and biodiversity indices between the different stages of *Rhododendron* shrubs. All plots were prepared using SigmaPlot 14.0.

3 Results

3.1 Effects of clearcutting on *Rhododendron* shrub community characteristics

The three communities comprised 26 species, including nineteen species of shrubs and seven species of herbaceous plants, belonging to 14 families and 22 genera (Tables 1, 2). Ericaceae, Rosaceae, and Theaceae accounted for the highest number of species, specifically 19.23%, 15.38%, and 11.54% of the total, respectively. Three species of *Rhododendron* plants accounted for 11.54% of the total species.

CK comprised 13 species belonging to seven families (including Ericaceae, Lauraceae, Theaceae, and Poaceae) and 11 genera. Four species were identified in the herbaceous layer and nine in the shrub layer of which five viz., *R. delavayi*, *L. ovalifolia*, *R. annae*, and *P. japonica* of Ericaceae and *L. pungens* of Lauraceae exhibited IVs > 0.1 (0.31, 0.17, 0.12, 0.12, and 0.12, respectively). *R. delavayi* was the dominant species in the shrub layer of CK, and *L. ovalifolia* was the subdominant species.

TABLE 1 Effects of clearcutting on species composition of *Rhododendron* shrub communities.

Layer	Family	Species name	Community		
			CK	D_{3yr}	D_{6yr}
Shrub	Ericaceae	*R. delavayi*	1	1	1
		R. annae	1	1	1
		R. lilacinum	1	1	1
		Lyonia ovalifolia	1	1	1
		Pieris japonica	1	1	1
	Rosaceae	*Rubus trianthus*	NA	1	1
		R. corchorifolius	NA	1	1
		Cotoneaster horizontalis	NA	1	1
		Pyracantha fortuneana	NA	NA	1
	Lauraceae	*Litsea pungens*	1	1	1
		Machilus pingii	1	NA	NA
	Theaceae	*Eurya japonica*	1	1	1
		E. loquaiana	NA	1	1
		Camellia oleifera	NA	1	1
	Salicaceae	*Populus adenopoda*	NA	1	1
		Salix matsudana	NA	1	1
	Pinaceae	*Pinus armandii*	1	NA	NA
	Fagaceae	*Castanea seguinii*	NA	1	1
	Smilacaceae	*Smilax china*	NA	1	1
Herbaceous	Poaceae	*Miscanthus floridulus*	1	1	1
		Fargesia spathacea	1	1	1
	Thelypteridaceae	*Macrothelypteris oligophlebia*	NA	1	NA
	Rosaceae	*Duchesnea indica*	NA	1	1
	Cyperaceae	*Cyperus rotundus*	1	1	NA
	Juncaceae	*Juncus effusus*	1	1	NA
	Asteraceae	*Elephantopus scaber*	NA	1	NA
Total	14	26	13	23	20

"NA" indicates that the species did not appear in the community, and "1" indicates that the species appeared in the community. CK, Community before clearcutting; D_{3yr}, Community 3 years after clearcutting; D_{6yr}, Community 6 years after clearcutting.

D_{3yr} comprised the highest number of species, with 23 species from 12 families (including Ericaceae, Rosaceae, Theaceae, and Poaceae) and 19 genera. There were seven species in the herbaceous layer and 16 in the shrub layer of which two, *R. delavayi* and *R. annae* of Ericaceae, exhibited IVs of > 0.1 (0.53 and 0.19, respectively). *R. delavayi* was the dominant species in the shrub layer of D_{3yr}, and *R. annae* was the subdominant species.

D_{6yr} comprised 20 species belonging to nine families (including Ericaceae, Rosaceae, Theaceae, and Poaceae) and 16 genera. There were three species in the herbaceous layer and seventeen in the shrub layer. Consistent with D_{3yr}, two species in the shrub layer, *R. delavayi* and *R. annae*, exhibited IVs > 0.1 (0.46 and 0.18, respectively). *R. delavayi* was the dominant species in the shrub layer of D_{6yr}, and *R. annae* was the subdominant species.

In the CK→D_{3yr}→D_{6yr} community sequence, the height and coverage of *Rhododendron* shrubs first decreased and then increased (Figure 1). The height decreased significantly from 191.87 cm in CK to 75.61 cm in D_{3yr} and then recovered to 116.71 cm in D_{6yr}. The coverage decreased significantly from 68.46% in CK to 37.89% in D_{3yr} and then increased significantly to 73.28% in D_{6yr}. The relative height increased from 43.79% in CK to 65.40% in D_{3yr} and then decreased to 58.54% in D_{6yr}. The relative coverage increased from 49.05% in CK to 83.24% in D_{3yr} and then decreased to 77.32% in D_{6yr}. The height of *Rhododendron* species in

TABLE 2 Effects of clearcutting on importance values (IVs) of species in the shrub layer of *Rhododendron* shrub communities.

Species name	IV		
	CK	D_{3yr}	D_{6yr}
R. delavayi	0.31	0.53	0.46
R. annae	0.12	0.19	0.18
R. lilacinum	0.02	0.02	0.02
Lyonia ovalifolia	0.17	0.04	0.07
Pieris japonica	0.12	0.02	0.03
Rubus trianthus	NA	0.03	0.04
R. corchorifolius	NA	0.01	0.01
Cotoneaster horizontalis	NA	0.03	0.04
Pyracantha fortuneana	NA	NA	0.00
Litsea pungens	0.12	0.01	0.02
Machilus pingii	0.09	NA	NA
Eurya japonica	0.04	0.04	0.05
E. loquaiana	NA	0.02	0.01
Camellia japonica	NA	0.00	0.01
Populus adenopoda	NA	0.01	0.01
Salix matsudana	NA	0.03	0.03
Pinus armandii	0.01	NA	NA
Castanea seguinii	NA	0.01	0.01
Smilax china	NA	0.01	0.01
Total: 19	9	16	17

"NA" indicates that the species did not appear in the community. CK, Community before clearcutting; D_{3yr}, Community 3 years after clearcutting; D_{6yr}, Community 6 years after clearcutting.

the three communities were significantly different ($p < 0.05$). The coverage in D_{3yr} was significantly different from that in CK and D_{6yr} ($p< 0.05$). The relative height and coverage in CK were both significantly different from those in D_{3yr} and D_{6yr} ($p < 0.05$).

3.2 Effects of clearcutting on the diversity of species in *Rhododendron* shrub communities

The Margalef richness index values of species in the shrub layers of the three communities were significantly different ($p < 0.05$) (Figure 2). However, the differences in the Simpson diversity, Shannon–Wiener diversity, and Pielou evenness indices were not significant ($p > 0.05$). The values of all four indices were the highest in CK and lowest in D_{3yr}. The values of the Margalef richness, Simpson diversity, Shannon–Wiener diversity, and Pielou evenness indices of species in D_{3yr} were 61.15%, 80.30%, 84.79%, and 96.61% of that of species in CK, respectively.

As CK→D_{3yr}→D_{6yr} progressed, the dissimilarity coefficients of the three communities showed a decreasing trend (Table 3). Both Cody and Whittaker indices were the highest in CK and D_{3yr} (3.83 and 1.65, respectively) and the lowest in D_{3yr} and D_{6yr} (0.83 and 1.20, respectively). The similarity indices, the Jaccard and Sorenson indices, were the highest in D_{3yr} and D_{6yr} (0.87 and 0.93, respectively) and the lowest in CK and D_{3yr} (0.38 and 0.55, respectively). The similarity between CK and D_{3yr} was low, that between CK and D_{6yr} was moderate, and that between D_{3yr} and D_{6yr} was high.

3.3 Effects of clearcutting on the renewal of *Rhododendron* shrub communities

The height and coverage as well as the sprouting time and age of *Rhododendron* shrubs were significantly and positively correlated ($p < 0.01$). The correlation degree of sprouting time was higher than that of the age of *Rhododendron* shrubs (Table 4).

The sprouting time (t) and age (a) are the two main factors that affect clearcutting sprouting of *Rhododendron* shrubs. The linear relationships between sprouting height (h), sprouting coverage (c), sprouting time (t), and age (a) of *Rhododendron* shrubs after clearcutting were well fitted ($R^2 = 0.65$, $p < 0.01$ and $R^2 = 0.50$, $p < 0.01$, respectively) (Table 5).

The height of *Rhododendron* shrubs in CK, D_{3yr}, and D_{6yr} showed a gradual increasing trend with age (Figure 3). Compared with CK, the height of *Rhododendron* shrubs in D_{3yr} and D_{6yr} was lesser and increased slowly. The coverage rates of *Rhododendron* shrubs in the three communities also increased gradually with increasing age. The coverage rates of *Rhododendron* shrubs in D_{3yr} and D_{6yr} at the early stage were higher than those in CK.

To determine the sprouting ability at different ages, the age of *Rhododendron* shrubs was divided into three classes (I, II, and III). The sprouting ability of *Rhododendron* shrubs first increased and then decreased with age (Figure 4). Class II *Rhododendron* shrubs had the strongest sprouting ability. Moreover, the sprouting ability of class III *Rhododendron* shrubs was significantly different from that of classes I and II shrubs ($p < 0.05$).

4 Discussion

4.1 Effects of clearcutting on species composition and community characteristics of *Rhododendron* shrubs

Species composition reflects the structure, dynamic changes, and succession characteristics of a community and plays a decisive role in community diversity (Gilliam, 2007; Liu et al., 2020). In this study, 26 species belonging to 14 families and 22 genera were identified in the three communities studied (Table 1). The number of species in CK was the lowest probably because the canopy density of *Rhododendron* shrubs was high and the litter layer was thick, which reduced the migration and colonisation of *Rubus trianthus*, *Cotoneaster horizontalis*, *Eurya loquaiana*, *Populus adenopoda*, belonging to the Rosaceae, Theaceae, Salicaceae, as well as herbaceous plants. However, clearcutting weakened interspecies

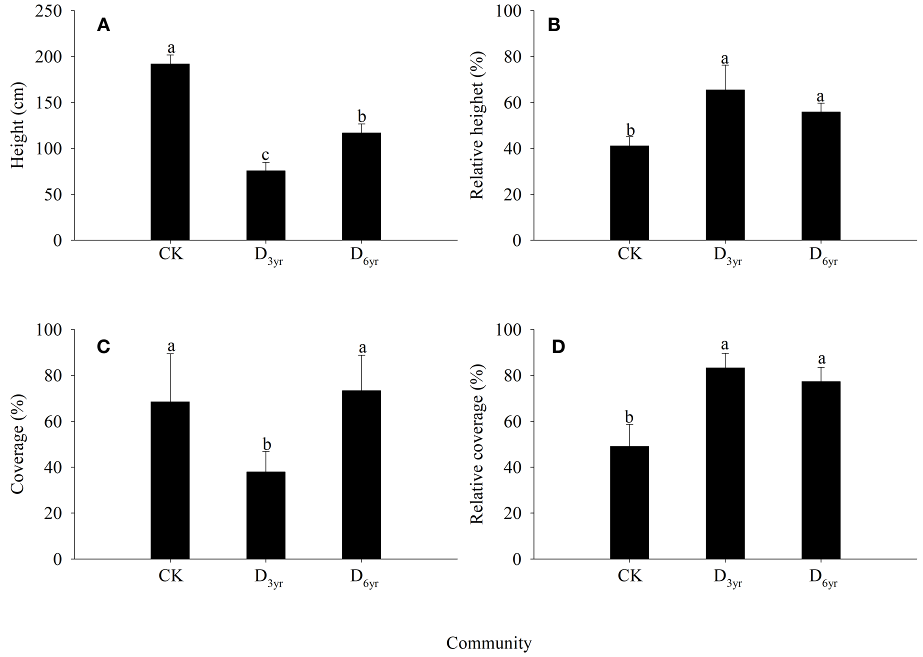

FIGURE 1
Effects of clearcutting on the height and coverage of *Rhododendron* shrubs. Height **(A)**; Relative height **(B)**; Coverage **(C)**; Relative coverage **(D)**. **(A–C)** indicate significant difference (p< 0.05). CK, control; D_{3yr}, community in 2018; D_{6yr}, community in 2021.

competition by reducing canopy density (Jones et al., 2019). Consequently, a large number of herbaceous plants, and species belonging to Rosaceae, Theaceae, and Salicaceae migrated; thus, D_{3yr} had the highest number of species. Subsequently, *Rhododendron* shrubs gradually occupied the upper space, the canopy density increased, and herbaceous plants gradually disappeared. Therefore, the number of species in D_{6yr} was lower compared with that in D_{3yr}.

The height and coverage of plants in communities are important indicators for evaluating the plant growth status (Chen et al., 2014). In this study, the height and coverage of plants in communities after clearcutting were significantly higher than those of plants in the seed

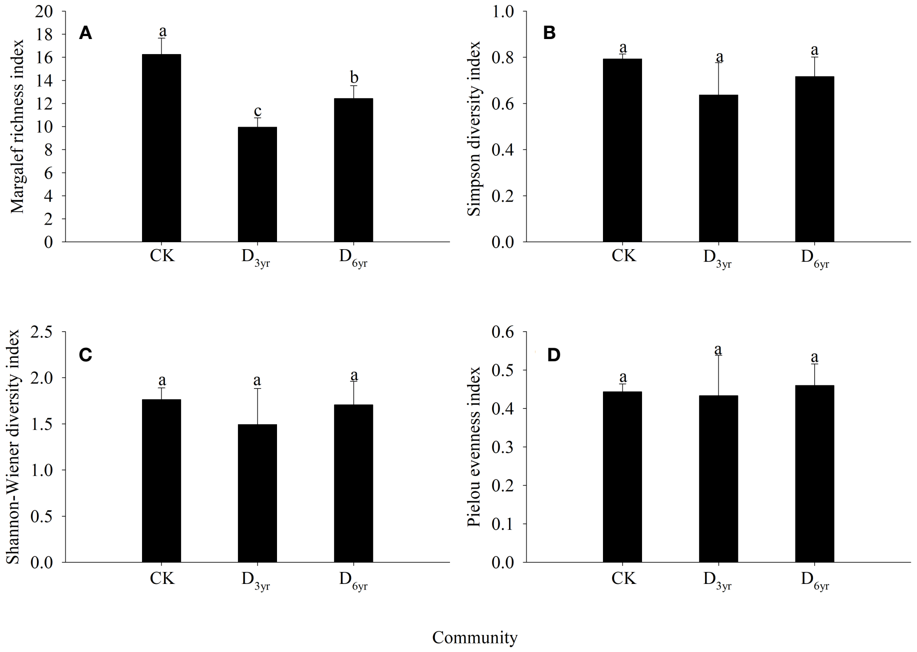

FIGURE 2
Effects of clearcutting on α-diversity of *Rhododendron* shrub communities. Margalef richness index **(A)**; Simpson diversity index **(B)**; Shannon–Wiener diversity index **(C)**; Pielou evenness index **(D)**. **(A–C)** significant difference (p< 0.05). CK, control; D_{3yr}, community in 2018; D_{6yr}, community in 2021.

TABLE 3 Effects of clearcutting on the β-diversity index of species in *Rhododendron* shrub communities.

Index	Community	CK	D_{3yr}	D_{6yr}
β_c	CK	0.00	3.83	3.50
	D_{3yr}	3.83	0.00	0.83
	D_{6yr}	3.50	0.83	0.00
β_{ws}	CK	0.00	1.65	1.55
	D_{3yr}	1.65	0.00	1.20
	D_{6yr}	1.55	1.20	0.00
C_j	CK	1.00	0.38	0.45
	D_{3yr}	0.38	1.00	0.87
	D_{6yr}	0.45	0.87	1.00
C_s	CK	1.00	0.55	0.62
	D_{3yr}	0.55	1.00	0.93
	D_{6yr}	0.62	0.93	1.00

β_c denotes the Cody index, β_{ws} denotes the Whittaker index, C_j denotes the Jaccard index, and C_s denotes the Sorensen index. CK, Community before clearcutting; D_{3yr}, Community 3 years after clearcutting; D_{6yr}, Community 6 years after clearcutting.

renewal communities (Figure 1), primarily because the large number of sprouting branches produced by *Rhododendron* shrubs could occupy more space by utilizing the resources, hence promoting rapid formation of community hierarchy. Post clearcutting, the sprouting coverage of *Rhododendron* shrubs in D_{6yr} was higher than that of shrubs in CK, primarily because clearcutting promoted shrub tillering and expanded individual canopy width. After clearcutting, the relative height of *Rhododendron* shrubs in D_{3yr} and D_{6yr} also increased significantly, probably because *Rhododendron* shrubs occupied the upper space of the whole shrub community after clearcutting, playing a dominant role in light absorption and utilization. The absence of other tall trees and shrub vegetation enabled *Rhododendron* plants roots to utilize soil nutrients more effectively. Therefore, clearcutting resulted in the domination of *Rhododendron* plants in the community, with vigorous population renewal and a stronger self-sustaining ability of the population.

4.2 Effects of clearcutting on the diversity of *Rhododendron* shrub communities

As a basic feature of a community, biodiversity is a key factor driving the dynamics and processes of an ecosystem and can indicate the habitat status, composition structure, and distribution pattern of a community (Liu and Bra, 1998; Tilman et al., 2012). In this study, the evenness index of the communities changed after clearcutting (Figure 2). The index value was relatively large, indicating that the heterogeneity of the study area was poor. This was also determined by the characteristics of the sprouting branches of *Rhododendron* shrubs. Although clearcutting increased the number of species, the α-diversity was still lower than that in CK before clearcutting. This may be because *Rhododendron* plants has a strong sprouting ability. After clearcutting, *Rhododendron* plants is likely to occupy space in the form of sprouting branches to inhibit the migration and colonisation of foreign species (Grant and Loneragan, 1999; Kruger and Midgley, 2001). Therefore, *Rhododendron* plants with its strong sprouting abilities can reduce species diversity and species turnover in the community to a certain extent.

TABLE 4 Correlation between sprouting height and coverage and time and age of *Rhododendron* shrubs.

	Height	Coverage
Time	0.69**	0.62**
Age	0.42**	0.37**

** indicates significant correlation at the 0.01 level.

TABLE 5 Regression model of sprouting height, sprouting coverage, and sprouting time of *Rhododendron* shrubs.

	Regression equation	R^2
Height	$h = 13.55t + 8.15a - 44.60$	0.65**
Coverage	$c = 0.60t + 0.37a - 3.43$	0.50**

** indicates significant correlation at the 0.01 level. h, sprouting height; t, sprouting time; a, age; and c, sprouting coverage.

β-Diversity is usually expressed as the turnover rate of biological species in different habitats. A high β-diversity index indicates a low level of species similarity between different habitats or ecosystems (Yang et al., 2020b). The results showed that the similarity between CK and D_{3yr} was low, that between CK and D_{6yr} was moderate, and that between D_{3yr} and D_{6yr} was high (Table 3). The Cody and Whittaker indices were higher before and after clearcutting, whereas the Jaccard and Sorenson indices were lower, indicating that clearcutting changed the species composition and community structure of *Rhododendron*. The similarity between CK and D_{3yr} was low but that between CK and D_{6yr} was moderate, indicating that with the progression of CK→D_{3yr}→D_{6yr}, the number of common plant species first decreased and then increased. Subsequently, the similarity among species composition also first decreased and then increased, indicating that *Rhododendron* plants could recover to the pre-clearcutting community level in a short time through clearcutting–sprouting renewal.

4.3 Effects of clearcutting on the renewal of *Rhododendron* shrub communities

In *Rhododendron* shrub communities, both seedlings and sprouting seedlings can undergo population renewal. Nevertheless, sprouting seedlings are an important source of population dynamics (Vesk and Westoby, 2004). Due to the strong sprouting ability of *Rhododendron* plants, deforested communities rapidly self-substitute, which not only affects the community structure but also has an important impact on population dynamics. Clearcutting–sprouting renewal avoids the problems of very low sprouting and survival rates as well as weak seedling competitiveness. The results of this study similarly showed that the dominance of the *Rhododendron* population in D_{3yr} and D_{6yr} after sprouting was greater than that

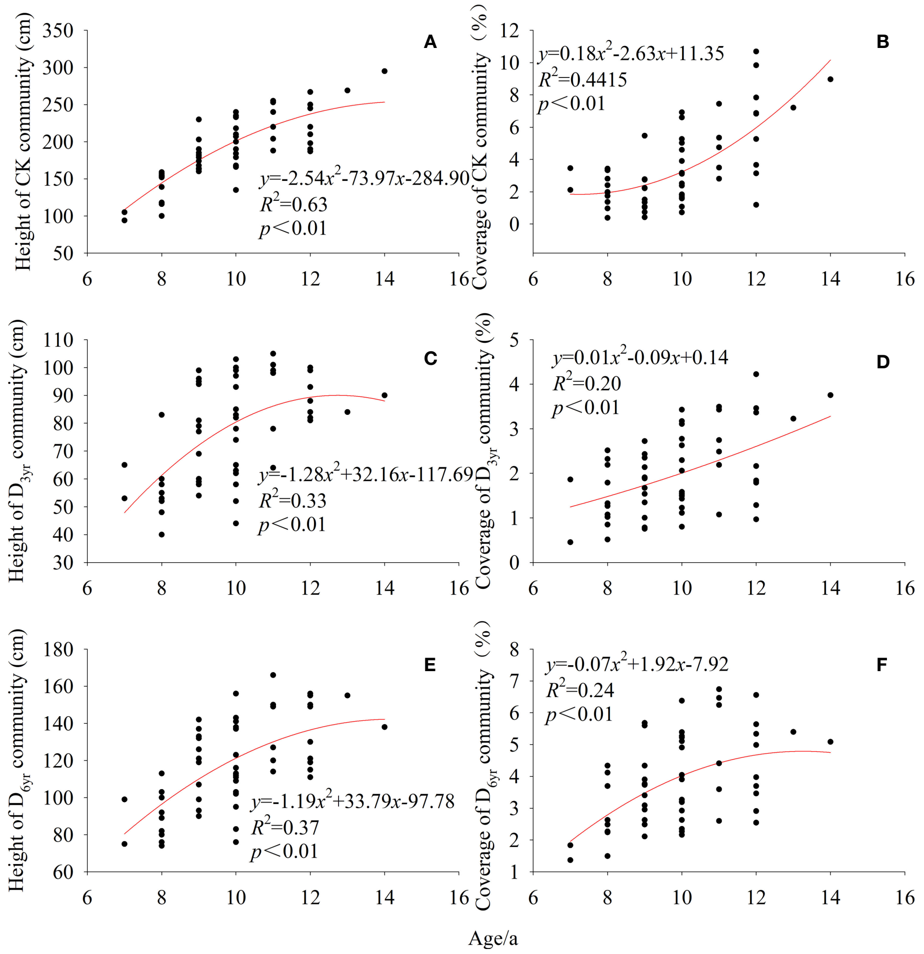

FIGURE 3
Variation in height and coverage of *Rhododendron* shrubs with age. Height of CK community **(A)**; Coverage of CK community **(B)**; Height of D_{3yr} community **(C)**; Coverage of D_{3yr} community **(D)**; Height of D_{6yr} community **(E)**; Coverage of D_{6yr} community **(F)**. CK, control; D_{3yr}, community in 2018; D_{6yr}, community in 2021.

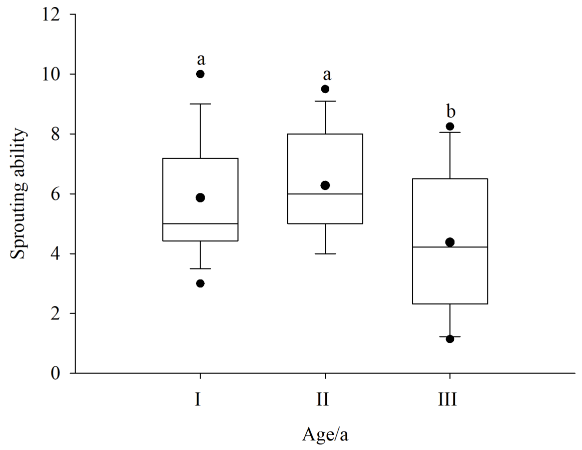

FIGURE 4
Effect of age of *Rhododendron* shrubs on sprouting ability. I, 7–9 years; II, 10–12 years; and III, > 12 years. a and b denote significant difference (p < 0.05).

in CK before clearcutting. The growth recovery of *Rhododendron* plants after clearcutting is completely dependent on the amount of stubble, root tiller, and rhizome, whereas the number of sprouts is a common index to characterize the strength of sprouting (Chi et al., 2019). Although the sprouting ability of *Rhododendron* plants was strong in this study, the recovery ability first increased and then decreased with the age of the *Rhododendron* shrubs. The sprouting ability of *Rhododendron* shrubs of age 10–12 years was the strongest (Figure 4). This may be associated with the aging of plants, an excessively large root system, and a lack of rhizome growth, which led to partial necrosis of the underground root system.

The community succession of *Rhododendron* plants does not deviate far from the original direction because of its strong sprouting ability and the effect of the ecological niche after clearcutting (Ahmad et al., 2021). However, the communities in this study had a high number and proportion of *Rhododendron* shrubs initially, which were *in situ* substituted with a similarly high number, accelerating the recovery to the original structure and succession rate of the community. Therefore, the shrub layer of *Rhododendron* communities after clearcutting was primarily composed of sprouting branches of *Rhododendron*, and the final direction of succession was subtropical evergreen broad-leaved forest. Compared with seed renewal and succession, the clearcutting–sprouting succession of *Rhododendron* plants takes a shorter time to achieve maturity (Loucks, 1970; Chen et al., 2019).

5 Conclusions

In total, 26 species from 22 genera and 14 families were found in the three communities. Clearcutting promoted the migration and colonisation of the families Rosaceae, Theaceae, and Salicaceae and other herbaceous plants, whereas the relative height and coverage of shrubs in the communities increased significantly. After clearcutting, there was a slight change in community evenness and a decrease in the α-diversity. The β-diversity showed that clearcutting improved the dominance of *Rhododendron* plants in the community and promoted sprouting renewal of *Rhododendron* populations. Moreover, the sprouting ability of *Rhododendron* shrubs of age 10–12 years was the strongest. Clearcutting did not affect the direction of community succession, but could accelerate the succession rate. Owing to the short observation period of clearcutting and sprouting of *Rhododendron* communities in this study, it was not possible to accurately predict the rate of population renewal and community succession of *Rhododendron* shrubs. In subsequent studies, multiple clearcutting modes and *Rhododendron* population succession stages will be established in combination with the competitive ability of the *Rhododendron* population.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

YZ, XZ, and LW contributed to the conception and design of the study. HS confirmed and guided the study. ZW, BJ, and HS carried out the experiments. YW performed the statistical analysis and wrote the first draft of the manuscript. YZ, XZ, and CC guided writing sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Climate and land-use changes threaten the effectiveness of protected areas for protecting Galliformes in Southeast Asia

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Climate and land-use changes and their interactions have a profound effect on biodiversity, especially in biodiverse areas such as Southeast Asia (SEA) where aggregations of endemic species are widespread. To increase the effectiveness of biodiversity protection, it is crucial to understand the effect of climate and land-use changes on biodiversity. In the present study, we predicted future land-use changes based on a Cellular automaton Markov chain model (CA-MARKOV), and took Galliformes species as an example to assess the impact of climate and land-use changes on the effectiveness of protected areas in SEA. In addition, we used an ensemble of species distribution models (SDMs) to assess the potential habitats and their dynamics of 62 Galliformes species currently and in the 2070s. Our results showed that climate and land-use changes would reduce the suitable habitats of these Galliformes species. Among them, 22 or 31 species would migrate upward because of a decrease in habitat suitability at lower elevations caused by climate and land-use changes, while other 40 or 30 species were predicted to migrate downward because of land use changes under two dispersal scenarios. These changes would expand the area with low and high diversity, but there would be a mismatch between the current protected areas (PAs) and future suitable habitats with high diversity. In order to effectively ensure biodiversity protection and conserve 30% of the planet by 2030, our findings suggest that we should establish new PAs or adjust the range of PAs based on the impact of climate and land-use changes.

KEYWORDS

climate change, land use, Galliformes, protected area, Southeast Asia

1 Introduction

Global warming and anthropogenic land-use changes are considered to have irreversible effects on biodiversity (Jetz et al., 2007; Pearce-Higgins et al., 2017), including suitable habitat range reduction (Brambilla et al., 2020), population decline (Powers and Jetz, 2019) and genetic diversity loss (Hu et al., 2021). Climate change usually affects the species distribution of mammals (Brodie, 2016; Hidasi-Neto et al., 2019), birds (Jetz et al., 2007; Lehikoinen and Virkkala, 2016), lizards (Jiang et al., 2023), etc. by reducing habitat suitability. Besides, it may aggravate the extinction risk of species (Urban, 2015; Manes et al., 2021). For instance, Sekercioglu et al. (2007) have predicted that 400–550 landbirds will be extinct as a result of future changes by 2100. Protected areas (PAs) are considered as refuges for species, and can mitigate the impact of climate change on species (Shen et al., 2015; Michalak et al., 2018). However, recent studies have suggested that current PAs will be challenged by future climate change (Kyprioti et al., 2021; Salvadeo et al., 2021), and may fail to provide enough space for species. Therefore, an accurate prediction of future species distribution is necessary for managers to develop policies that can mitigate the impact of future climate change on species.

Moreover, landscape patterns also need to be considered in the prediction of future species distribution. A previous study has predicted that 1700 species of mammals, birds and amphibians may lose suitable habitats due to land-use changes between 2015 and 2070 (Powers and Jetz, 2019). Current land-use changes such as road construction, urbanization and transforming natural habitats into farmland can influence habitat connectivity (Krauss et al., 2010; Hansen et al., 2013; Wilson et al., 2015; Tang et al., 2020). Habitats changed by human activity were hereinafter referred to as “altered habitats”. Although several species of birds have been demonstrated to inhabit altered habitats or edges between natural and altered habitats (Kark et al., 2007; Møller et al., 2012; Carlen et al., 2021), most wild species have suffered habitat loss due to land-use changes (Powers and Jetz, 2019; Shahabuddin et al., 2021).

In addition, climate and land-use changes are widely observed to have a combined influence on species (Côté et al., 2016; Keshtkar and Voigt, 2016; Symes et al., 2018; Northrup et al., 2019; Bühne et al., 2021). The interactions between climate and land-use changes are predicted to have more negative impacts on species than any single factor (Symes et al., 2018; Northrup et al., 2019; Bühne et al., 2021). The increased quantity of manmade landscapes is attributed to declining natural habitats, increased CO_2 emissions and accelerated global warming (Kucuker et al., 2015). Habitat loss has especially disastrous consequences for forest-dependent species (Gaüzère et al., 2020; Hülber et al., 2020), and climate change further aggravates the impact of land-use changes on species with specific geographic ranges and migration abilities (Jetz et al., 2007; Brodie, 2016; Dai et al., 2021). Ignoring the combined influence of climate and land-use changes on biodiversity may result in an underestimation of the situation, whereas examining the combined impacts of these variables can provide a better prediction for species conservation (Titeux et al., 2016; Northrup et al., 2019).

Southeast Asia (SEA) is a world-famous biodiversity hotspot with abundant forest resource. However, people have been transforming forest into farmland and towns for survival and economic development, which led to the loss and fragmentation of forests (Estoque et al., 2019). These undoubtedly exacerbated the loss of biodiversity, and it seems unstoppable (Sodhi et al., 2010). Galliformes is an important component of biodiversity and they have a high value in economy and culture for residents of SEA. Therefore, they were often regarded as the main targets of hunters (Savini et al., 2021). According to the records, SEA encompassed the habitat range of 77 Galliformes species, and about 27% of them are at risk of extinction (IUCN, 2023). Unfavorable forest transformation always had negative effects on Galliformes species that inhabit forest landscapes (Grainger et al., 2018; Savini et al., 2021), and it directly changed land-use patterns and indirectly accelerates global warming (Bos et al., 2020). These changes will aggravate the survival pressure of Galliformes. Protected areas were powerful tools for protecting wildlife and their habitat (UNEP-WCMC, 2022), Previous study showed that intensities of human interference in protected areas of SEA are greater than that of other regions in the world (Geldmann et al., 2019), and protected areas could not protect the intact forests effectively in SEA (Potapov et al., 2017). Galliformes were often taken as indicators of habitat conditions (Bagaria et al., 2021), and because of their extinction risk, they also were used to evaluate the conservation status of SEA (Grainger et al., 2018). Therefore, evaluating how the Galliformes species inhabiting forest landscapes respond to climate and land-use changes is crucial to assess the conservation status of SEA and formulate management measures. Here, we assessed the potential habitats of Galliformes species and their variations under climate and land-use changes in SEA. We aimed to: 1) evaluate the impact of climate and land-use changes on the distribution of Galliformes species; 2) predict the changes in species diversity; and 3) identify conservation gaps and provide suggestions for future protection.

2 Materials and methods

2.1 Study area and species data collection

SEA encompassed countries (Figure 1) including the Republic of the Union of Myanmar (MMR), Thailand (THA), Brunei Darussalam (BRN), Lao People’s Democratic Republic (LAO), Cambodia (KHM), the Socialist Republic of Vietnam (VNM), Malaysia (MYS), the Republic of Singapore (SGP), the Republic of Indonesia (IDN), the Republic of the Philippines (PHL) and the Democratic Republic of Timor-Leste (TMP) (Grainger et al., 2018; Savini et al., 2021).

We identified 77 native Galliformes species distributed in SEA and verified species whether is extinct or introduced in 11 countries according to IUCN Red List, also collected the occurrence data of them from Global Biodiversity Information Facility (GBIF.org, 2021), ebirds (https://ebird.org/) and inaturalist (https://www.inaturalist.org/) from 2000 to 2020. To develop the effectiveness of these data (Meyer et al., 2016; Stropp et al., 2016), we excluded points that were not displayed in A Checklist on the Classification and Distribution of the Birds of the World (Second Edition) (Zheng, 2021), and deleted the repetitive and default (NA

FIGURE 1
Location of eleven countries of Southeast Asia in our study.

value) points. Specifically, red junglefowl (*Gallus gallus*) was not considered in our study due to the possibility of misidentification between wild and domestic individuals during observation. We excluded species with less than 10 individuals. As a result, we obtained a total of 7701 points of 62 species for further analysis (Appendix. Table B.1).

2.2 Environmental variables

2.2.1 Climatic variables

Climate change can alter the climate niche of species (Selwood and Zimmer, 2020). To describe the potential effect of future climate change on Galliformes species in SEA, we compared the species distribution areas of Galliformes species between current and future climate conditions. We downloaded 19 bioclimatic variables from WorldClim 2.1 (at 1 km resolution; https://www.worldclim.org/), and they were used to represent the current climate conditions. These 19 bioclimatic variables represented annual trends (e.g., mean annual temperature and annual precipitation), seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperature in the coldest and warmest months, and precipitation during the wet and dry quarters) (Fick, 2017), and were also related to the distribution of Galliformes species (Johnsgard, 1999). We also downloaded these 19 bioclimatic variables during 2061–2080 (the 2070s), and they were used to represent the future climate conditions, which covered three Shared Socioeconomic Pathways (SSP) and the Representative Concentration Pathways (RCP), including SSP126, SSP370 and SSP585. SSP126 was the combination of SSP1 and RCP 2.6, representing a low level of greenhouse gas emissions; SSP370 was the combination of SSP3 and RCP 7.0, representing a medium level of greenhouse gas emissions; and SSP585 was the combination of SSP5 and RCP 8.5, representing a high level of greenhouse gas emissions. Climatic datasets were obtained using the Beijing Climate Center Climate System Model (BCC-CSM2-MR) based on the Coupled Model Intercomparison Project (CMIP6).

2.2.2 Projection of land use and land cover changes

The Cellular automaton Markov chain model (CA-MARKOV) was used to evaluate the land use and land cover change (LULCC) from 2020 to 2080. This model combines CA method and the Markov chain model, and is widely used to predict effectively spatiotemporal changes in LULCC (Halmy et al., 2015). The CA-MARKOV model predicts future changes by quantifying the changes in LULCC between two periods (Mansour et al., 2022). First, we obtained the land cover data for 2000, 2010 and 2020 from the European Space Agency (at 300m resolution; https://cds.climate.copernicus.eu/). Next, we used the Markov chain model to calculate the transition probability and the transition area matrixes from to 2000 to 2010. Then, we used the CA-MARKOV method to test the spatial changes in cell condition and predict the spatial changes in 2020, and generated the prediction map (we refer to this as “2020p” hereinafter). The Kappa index was used to compare the similarity between 2020 and 2020p. The greater the value of the Kappa index, the more accurate the prediction (Gidey et al., 2017). We further predicted the LULCC in the 2070s (Powers and Jetz, 2019). The model processes are as follows:

$$S(t+1) = P_{ij} * S(t) \tag{1}$$

$$\| P_{ij} \| = \begin{Vmatrix} P_{1,1} & P_{1,2} & \cdots & P_{1,n} \\ P_{2,1} & P_{2,2} & \cdots & P2,n \\ \vdots & \vdots & \ddots & \vdots \\ P_{n,1} & P_{n,2} & \cdots & P_{n,n} \end{Vmatrix} \tag{2}$$

where S(t)/S(t+1) represents the land use status at time t and t+1, while P_{ij} is the transition probability matrix in a state, representing the possibility of converting from current states i to another state j at time n; Range of P_{ij} is from 0 to 1, and the higher the value, the higher transition possibility.

2.2.3 Other environmental variables

Other environmental variables were used in our model including Topographic Position Index (TPI), slope and aspect. We collected the Digital Elevation Model (DEM) from SRTM (at 30m resolution; https://srtm.csi.cgiar.org). Slope and aspect were extracted from DEM by ArcGIS 10.6. The neighborhood of TPI adopted the rectangle (both of width and height are 3 pixels), and the calculation formula of TPI is as follows:

$$TPI = E - \overline{E}$$

where E represents the elevation of a point; $\overline{E}$ represents the mean elevation of areas around this point. We kept these variables stable in future analysis.

2.3 Data analysis

2.3.1 Spatial resolution of environmental variables

All variables were in raster format, and we resampled them to 1 km resolution under GCS_WGS_1984. Variance Inflation Factor (VIF) was used to deal with the collinearity of environmental variables. The variables with VIF values > 10 were excluded from the analysis.

2.3.2 Species distribution model formulation process

Species distribution models (SDMs) are widely used to predict a species' current and future distribution and habitat occupancy (Phillips et al., 2006; Jones-Farrand et al., 2011; Dai et al., 2021). Previous studies have shown that the predictions or projections from a single SDM may face challenges, and combining multiple SDMs (the ensemble approach) can increase the credibility of the model output (Araujo and New, 2007; Jones-Farrand et al., 2011; Kindt, 2018). RF and Maxent have been proved to have strong prediction ability (Phillips et al., 2006; Prasad et al., 2006). We assembled random forest (RF) and maximum entropy (Maxent) to predict the suitable habitat using the "sdm" package in R v.4.0.3 (Naimi and Araújo, 2016). We created a data object with species spatial points (the longitude and latitude) and predictors (retained environmental variables). The spatial points were presence-only data, and predictors were raster layers with the same spatial resolution, extent, and dimensions. In general, the absence data can be confirmed when there is sufficient evidence, but it is difficult to achieve this for living animals (Lobo and Tognelli, 2011). Therefore, we set 1000 random background points to obtain the pseudo-absence points in the same research area. Two SDMs were run as follows: 1) we randomly selected 70% of the species points for training each model, while the remaining 30% of species points were used for testing the performance of each model; 2) 10-fold cross-validation were performed to evaluate the model (Sill and Dawson, 2021). 3) The accuracy of SDMs was evaluated by the area under curve (AUC) of the receiver operating characteristic (ROC) curve; 4) Mean of the relative importance of variables was calculated based on AUC; 5) Suitable habitats of the prediction of two SDMs were assembled based on a weighted averaging that was weighted by the AUC statistic. We then used the output of fitting to project into 2070s.

2.3.3 Dispersal scenarios

Considering the dispersal behavior of species under future, we set two scenarios to identify the species suitable habitats (Feeley and Silman, 2010a), First, we assumed the Galliformes can dispersal to all potential habitat as "perfect dispersal scenarios". Secondly, we assumed Gallidormes have the limited dispersal abilities and created a ~111 Km buffer as "limited dispersal scenarios"(Namkhan et al., 2022).

2.3.4 Changes in distribution

To understand the ecological impacts of climate change and LULCC on the distribution of Galliformes, we converted the prediction of SDMs into a binary variable (suitable or unsuitable) map by adopting the average logistic threshold value of maximum training sensitivity plus specificity. And suitable habitat losses and gains were calculated by current and future binary map. Mann–Whitney U test (variables did not pass the test for homogeneity of variance) was adopted to compare the difference in vertical distribution of species between current and future scenarios. Judgment criteria for changes in vertical distribution were shown in Appendix Table A.1. We overlapped future suitable habitat of 62 Galliformes species and used Natural breaks methods to classified them into four diversity levels (low, general, median and high) based on the number of species. Finally, we overlapped the future binary maps and the PAs that were downloaded from the Protected Planet database (https://www.protectedplanet.net/en) to identify the gaps in the current protection areas.

3 Results

3.1 Model performance

The AUC values of each SDM were greater than 0.70, indicating good predictive ability of the SDMs (Appendix Figure A.1). There were no difference in predictive ability between Maxent and RF

(P >0.05). The value of Kappa for the projection by CA-MARKOV was 0.828, suggesting better predictive ability for land-use changes. The CA-MARKOV model predicted that the area of urban area, cropland, shrubland and grassland would significantly increase, while that of forest and water would decrease in the 2070s (Appendix Table.A.2). Variables retained in 62 SDMs were shown in Appendix Table B.2. Land use and precipitation of warmest quarter (Bio18) were the main factors affecting the habitat distribution of Galliformes in SEA (Appendix Figure A.2).

3.2 Suitable habitats of Galliformes under future conditions

Currently, the suitable habitat area for 62 Galliformes species ranged from 213 km^2 to 4,696,502 km^2 under perfect dispersal scenarios, and ranged from 191 km^2 to 1,100,116 km^2 under limited dispersal scenarios (Table 1). At perfect dispersal scenarios, SDMs showed that the suitable habitat area for 53 species would decrease under three future scenarios, while that for other 9 species would

TABLE 1 Current habitat area under two dispersal scenarios.

Species	Latin name	Perfect dispersal scenarios	Limited dispersal scenarios
		Area (km^2)	Area (km^2)
Asian Blue Quail	*Synoicus chinensis*	1,573,342	1,050,468
Bar-backed Partridge	*Arborophila brunneopectus*	295,060	251,944
Biak Scrubfowl	*Megapodius geelvinkianus*	3,855	1,931
Black-billed Brush-turkey	*Talegalla fuscirostris*	213	191
BloodPheasant	*Ithaginis cruentus*	305,720	14,258
Blyth’s Tragopan	*Tragopan blythii*	486,647	35,457
Bornean Crested Fireback	*Lophura ignita*	463,542	243,181
Bornean Partridge	*Arborophila hyperythra*	56,631	27,990
Bornean Peacock-pheasant	*Polyplectron schleiermacheri*	938,208	133,173
Bronze-tailed Peacock Pheasant	*Polyplectron chalcurum*	436,779	125,660
Brown Quail	*Synoicus ypsilophorus*	286,502	77,740
Bulwer’s Pheasant	*Lophura bulweri*	349,402	169,185
Chestnut-bellied Partridge	*Arborophila javanica*	24,326	21,172
Chestnut-headed Partridge	*Arborophila cambodiana*	1,722,566	90,399
Chestnut-necklaced Partridge	*Arborophila charltonii*	277,098	90,748
Chinese Francolin	*Francolinus pintadeanus*	1,221,800	1,100,116
Collared Brush-turkey	*Talegalla jobiensis*	343,857	54,265
Common Quail	*Coturnix coturnix*	176,962	25,404
Crested Argus	*Rheinardia nigrescens*	263,562	73,095
Crested Partridge	*Rollulus rouloul*	697,647	351,356
Crimson-headed Wood Partridge	*Haematortyx sanguiniceps*	71,097	23,204
Dusky Scrubfowl	*Megapodius freycinet*	80,054	33,673
Ferruginous Partridge	*Caloperdix oculeus*	376,379	118,930
Germain’s Peacock-pheasant	*Polyplectron germaini*	194,796	122,996
Great Argus	*Argusianus argus*	842,916	556,457
Green Junglefowl	*Gallus varius*	120,573	90,262
Green Peafowl	*Pavo muticus*	955,851	759,374
Green-legged Partridge	*Arborophila chloropus*	4,696,502	963,012
Grey Peacock-pheasant	*Polyplectron bicalcaratum*	351,947	291,781
Grey-breasted Partridge	*Arborophila orientalis*	37,189	19,419

(Continued)

TABLE 1 Continued

Species	Latin name	Perfect dispersal scenarios	Limited dispersal scenarios
		Area (km^2)	Area (km^2)
Hill Partridge	*Arborophila torqueola*	158,028	69,394
Japanese Quail	*Coturnix japonica*	992,843	239,974
Kalij Pheasant	*Lophura leucomelanos*	284,980	218,867
Lady Amherst's Pheasant	*Chrysolophus amherstiae*	12,196	813
Long-billed Partridge	*Rhizothera longirostris*	152,065	48,334
Malay Crested Fireback	*Lophura rufa*	778,067	48,292
Malay Crestless Fireback	*Lophura erythrophthalma*	410,454	97,140
Malay Partridge	*Arborophila campbelli*	32,255	8,100
Malay Peacock-pheasant	*Polyplectron malacense*	89,478	55,403
Maleo	*Macrocephalon maleo*	146,779	73,020
Moluccan Scrubfowl	*Eulipoa wallacei*	306,068	43,151
Mountain Bamboo-partridge	*Bambusicola fytchii*	259,075	131,797
Mountain Peacock-pheasant	*Polyplectron inopinatum*	89,565	45,122
Mrs Hume's Pheasant	*Syrmaticus humiae*	118,104	83,186
New Guinea Scrubfowl	*Megapodius decollatus*	534,913	63,189
Orange-footed Scrubfowl	*Megapodius reinwardt*	217,436	81,418
Orange-necked Partridge	*Arborophila davidi*	3,842,640	96,068
Palawan Peacock-pheasant	*Polyplectron napoleonis*	20,415	10,295
Philippine Scrubfowl	*Megapodius cumingii*	549,611	154,562
Rain Quail	*Coturnix coromandelica*	486,820	418,393
Red-billed Brush-turkey	*Talegalla cuvieri*	36,421	17,146
Red-billed Partridge	*Arborophila rubrirostris*	87,042	56,176
Rufous-throated Partridge	*Arborophila rufogularis*	492,051	297,477
Salvadori's Pheasant	*Lophura inornata*	179,063	61,689
Siamese Fireback	*Lophura diardi*	261,786	195,279
Silver Pheasant	*Lophura nycthemera*	646,344	350,595
Snow Mountain Quail	*Synoicus monorthonyx*	739,899	63,088
Sula Scrubfowl	*Megapodius bernsteinii*	19,095	3,729
Tan-breasted Partridge	*Arborophila rolli*	112,355	39,054
Tanimbar Scrubfowl	*Megapodius tenimberensis*	3,640	2,545
Wattled Brush-turkey	*Aepypodius arfakianus*	64,946	17,631
White-cheeked Partridge	*Arborophila atrogularis*	103,643	81,255

increase (Figure 2A). There were differences in proportion of habitat gain and loss between countries, but no differences in proportion of habitat gain or loss between future scenarios (Figure 3). Laos showed a significantly higher proportion of habitat gain than Malaysia, Myanmar, Thailand, Vietnam, Indonesia and Philippines. Brunei, EastTimor and Singapore had a significantly higher proportion of habitat gain than Indonesia and Philippines (Figure 3A). And Singapore exhibited a higher proportion of habitat loss than other countries (Figure 3B).

At limited dispersal scenarios, SDMs showed that the suitable habitat area for 43 species would decrease under three future scenarios, while that for other 19 species would increase

FIGURE 2
Proportion of habitat change under future scenarios. **(A)** Perfect dispersal scenarios; **(B)** Limited dispersal scenarios.

(Figure 2B). There were also differences in proportion of habitat gain and loss between countries, but no differences in proportion of habitat gain or loss between future scenarios (Figure 3). Brunei showed a higher proportion of habitat gain than other countries (Figure 3C). Cambodia, Laos and Vietnam exhibited a higher proportion of habitat loss than other countries (Figure 3D).

3.3 Vertical distribution of Galliformes under future conditions

There were differences in the elevation of potential habitats between current and future scenarios. At perfect dispersal scenarios, 22 species would move upward in the future, because of habitat gain at higher elevations (Table 2). Other 40 species would move downward in the future, because of habitat gain at lower elevations or habitats loss at higher elevations (Table 2). At limited dispersal scenarios, 31 species would move upward in the future, because of habitat gain at higher elevations (Table 3). Other 30 species would move downward in the future, because of habitat gain at lower elevations or habitats loss at higher elevations (Table 3).

3.4 Changes in species diversity and gap analysis

There was a significant difference in species diversity between current and future scenarios (Figures 4, 5). SDMs predicted that the area with general and medium diversity levels would obviously decrease under future scenarios, while the area with high and low diversity levels would increase.

At perfect dispersal scenarios, 15.53% of the suitable habitats were protected by PAs in 2020, while 16.52%, 16.48% and 16.50% of the suitable habitats would be protected by PAs under SSP126, SSP370 and SSP585. At limited dispersal scenarios, 90.89% of the suitable habitats were protected by PAs in 2020, while 21.66%, 21.15% and 20.43% of the suitable habitats would be protected by PAs under SSP126, SSP370 and SSP585.

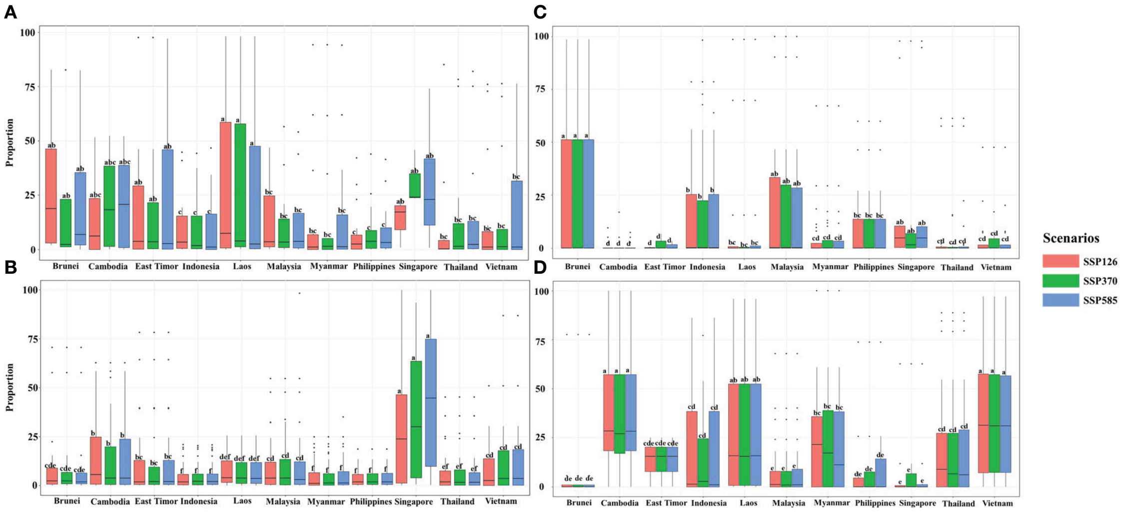

FIGURE 3
The difference in changes in suitable habitat between countries. **(A)** Proportion of habitat gain under perfect dispersal scenarios; **(B)** Proportion of habitat loss under perfect dispersal scenarios; **(C)** Proportion of habitat gain under limited dispersal scenarios; **(D)** Proportion of habitat loss under limited dispersal scenarios.

TABLE 2 Changes in elevation between current and future scenarios under perfect dispersal scenarios.

Species	Latin name	Current elevation	SSP126		SSP370		SSP585		Changes
			$Gain_E$	$Loss_E$	$Gain_E$	$Loss_E$	$Gain_E$	$Loss_E$	
Asian Blue Quail	*Synoicus chinensis*	335.25	418.70	504.10	423.15	503.34	172.42	453.35	-
Bar-backed Partridge	*Arborophila brunneopectus*	846.89	/	736.95	/	736.95	/	736.95	+
Biak Scrubfowl	*Megapodius geelvinkianus*	228.89	/	490.55	/	490.55	/	490.55	-
Black-billed Brush-turkey	*Talegalla fuscirostris*	50.49	/	106.35	/	106.35	/	106.35	-
BloodPheasant	*Ithaginis cruentus*	411.94	393.96	439.77	304.95	506.15	267.48	436.24	-
Blyth's Tragopan	*Tragopan blythii*	508.68	581.84	530.50	561.52	484.67	537.32	484.58	+
Bornean Crested Fireback	*Lophura ignita*	231.72	/	277.73	/	277.73	/	277.73	-
Bornean Partridge	*Arborophila hyperythra*	1146.41	/	1267.73	/	1267.73	/	1267.73	-
Bornean Peacock-pheasant	*Polyplectron schleiermacheri*	88.85	454.71	21.54	505.49	27.77	493.23	26.78	+
Bronze-tailed Peacock Pheasant	*Polyplectron chalcurum*	1150.92	/	1360.16	/	1360.16	/	1360.16	-
Brown Quail	*Synoicus ypsilophorus*	272.59	/	248.80	/	248.80	/	248.82	+
Bulwer's Pheasant	*Lophura bulweri*	688.48	/	838.45	/	838.45	/	838.45	-
Chestnut-bellied Partridge	*Arborophila javanica*	1042.81	/	891.94	/	925.57	/	918.95	+
Chestnut-headed Partridge	*Arborophila cambodiana*	709.67	/	365.51	/	365.77	/	365.83	+
Chestnut-necklaced Partridge	*Arborophila charltonii*	326.12	/	219.60	/	219.60	/	219.60	+
Chinese Francolin	*Francolinus pintadeanus*	393.78	/	317.65	/	317.65	/	317.65	+
Collared Brush-turkey	*Talegalla jobiensis*	136.35	243.01	98.55	292.49	98.55	319.12	98.53	+
Common Quail	*Coturnix coturnix*	230.81	265.87	280.47	229.38	301.63	192.75	276.13	-
Crested Argus	*Rheinardia nigrescens*	311.15	/	434.34	/	434.34	/	434.34	-
Crested Partridge	*Rollulus rouloul*	390.37	/	423.23	/	423.23	/	423.23	-

(Continued)

TABLE 2 Continued

Species	Latin name	Current elevation	SSP126		SSP370		SSP585		Changes
			Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	
Crimson-headed Wood Partridge	*Haematortyx sanguiniceps*	1156.63	/	1176.65	/	1176.65	/	1176.65	-
Dusky Scrubfowl	*Megapodius freycinet*	157.38	/	169.40	/	169.40	/	169.40	-
Ferruginous Partridge	*Caloperdix oculeus*	824.47	/	823.55	/	823.55	/	823.55	-
Germain's Peacock-pheasant	*Polyplectron germaini*	319.95	/	258.41	/	258.41	/	258.41	+
Great Argus	*Argusianus argus*	354.35	/	351.18	/	351.18	/	351.18	+
Green Junglefowl	*Gallus varius*	458.03	/	486.39	/	486.39	/	486.39	-
Green Peafowl	*Pavo muticus*	409.79	792.63	396.50	828.04	395.73	484.57	395.89	+
Green-legged Partridge	*Arborophila chloropus*	404.02	/	417.51	/	417.51	/	417.51	-
Grey Peacock-pheasant	*Polyplectron bicalcaratum*	901.44	/	972.29	/	972.29	/	972.29	-
Grey-breasted Partridge	*Arborophila orientalis*	661.14	/	1120.61	/	1120.61	/	1120.61	-
Hill Partridge	*Arborophila torqueola*	1620.76	/	1621.28	/	1621.28	/	1621.28	-
Japanese Quail	*Coturnix japonica*	148.34	496.68	183.40	497.93	171.99	490.16	170.99	+
Kalij Pheasant	*Lophura leucomelanos*	589.65	/	803.71	/	803.71	/	803.71	-
Lady Amherst's Pheasant	*Chrysolophus amherstiae*	242.86	294.16	255.64	270.58	250.42	259.54	257.36	+
Long-billed Partridge	*Rhizothera longirostris*	497.41	455.79	443.51	416.88	555.75	420.77	491.34	-
Malay Crested Fireback	*Lophura rufa*	256.53	321.84	240.14	365.63	238.38	319.37	227.00	+
Malay Crestless Fireback	*Lophura erythrophthalma*	126.51	610.00	126.45	592.12	125.99	613.43	124.90	+
Malay Partridge	*Arborophila campbelli*	1509.49	637.65	1602.81	637.65	1602.81	605.98	1603.38	-
Malay Peacock-pheasant	*Polyplectron malacense*	272.44	/	332.64	/	332.64	/	332.64	-
Maleo	*Macrocephalon maleo*	554.51	/	583.52	/	583.52	/	583.52	-
Moluccan Scrubfowl	*Eulipoa wallacei*	459.32	/	475.29	/	475.29	/	475.29	-
Mountain Bamboo-partridge	*Bambusicola fytchii*	1220.83	/	1100.13	/	1100.13	/	1100.13	+
Mountain Peacock-pheasant	*Polyplectron inopinatum*	417.32	191.36	940.95	260.59	751.09	736.74	815.23	-
Mrs Hume's Pheasant	*Syrmaticus humiae*	1007.16	/	1064.30	/	1064.30	/	1064.30	-
New Guinea Scrubfowl	*Megapodius decollatus*	359.95	410.07	406.68	438.75	398.81	417.86	407.14	+
Orange-footed Scrubfowl	*Megapodius reinwardt*	233.85	/	260.95	/	260.95	/	260.95	-
Orange-necked Partridge	*Arborophila davidi*	414.80	/	243.71	/	243.71	/	243.71	+
Palawan Peacock-pheasant	*Polyplectron napoleonis*	245.44	/	330.88	/	330.88	/	330.88	-
Philippine Scrubfowl	*Megapodius cumingii*	272.75	/	319.83	/	319.83	/	319.83	-
Rain Quail	*Coturnix coromandelica*	169.57	/	133.79	/	133.79	/	133.79	+
Red-billed Brush-turkey	*Talegalla cuvieri*	310.55	/	371.14	/	371.14	/	371.14	-
Red-billed Partridge	*Arborophila rubrirostris*	1448.62	/	1415.07	/	1415.07	/	1415.07	+
Rufous-throated Partridge	*Arborophila rufogularis*	979.75	/	1239.47	/	1239.47	/	1239.47	-
Salvadori's Pheasant	*Lophura inornata*	1269.27	/	1428.14	/	1428.14	/	1428.14	-
Siamese Fireback	*Lophura diardi*	316.21	/	371.04	/	371.04	/	371.04	-
Silver Pheasant	*Lophura nycthemera*	922.91	/	1013.62	/	1013.79	/	1013.80	-
Snow Mountain Quail	*Synoicus monorthonyx*	554.23	/	3157.86	/	3157.86	/	3157.86	-
Sula Scrubfowl	*Megapodius bernsteinii*	117.15	/	223.85	/	223.85	/	223.85	-

(Continued)

TABLE 2 Continued

Species	Latin name	Current elevation	SSP126		SSP370		SSP585		Changes
			Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	
Tan-breasted Partridge	*Arborophila rolli*	1451.66	/	1479.88	/	1479.88	/	1479.88	-
Tanimbar Scrubfowl	*Megapodius tenimberensis*	68.06	196.87	95.44	261.51	86.77	230.94	94.03	+
Wattled Brush-turkey	*Aepypodius arfakianus*	1081.00	455.06	898.16	675.02	898.32	500.28	898.45	-
White-cheeked Partridge	*Arborophila atrogularis*	571.19	225.70	546.24	142.49	547.03	196.30	546.10	-

TABLE 3 Changes in elevation between current and future scenarios under limited dispersal scenarios.

Species	Latin name	Current elevation	SSP126		SSP370		SSP585		Changes
			Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	
Asian Blue Quail	*Synoicus chinensis*	319.84	370.16	/	370.16	/	370.16	/	+
Bar-backed Partridge	*Arborophila brunneopectus*	631.59	/	735.25	/	735.25	/	735.25	–
Biak Scrubfowl	*Megapodius geelvinkianus*	703.45	751.89	/	751.89	/	751.89	/	+
Black-billed Brush-turkey	*Talegalla fuscirostris*	1218.23	1350.74	1467.17	1392.82	1487.22	1259.90	1526.13	–
BloodPheasant	*Ithaginis cruentus*	2399.26	3572.71	2813.91	3428.11	2815.84	3435.68	2816.67	+
Blyth's Tragopan	*Tragopan blythii*	213.69	/	183.31	/	183.31	/	183.31	+
Bornean Crested Fireback	*Lophura ignita*	645.57	/	574.53	/	576.58	/	577.64	+
Bornean Partridge	*Arborophila hyperythra*	299.82	/	237.39	/	237.39	/	237.39	+
Bornean Peacock-pheasant	*Polyplectron schleiermacheri*	129.92	504.60	32.78	515.01	36.30	551.63	34.32	+
Bronze-tailed Peacock Pheasant	*Polyplectron chalcurum*	904.61	593.35	/	593.35	/	593.35	/	–
Brown Quail	*Synoicus ypsilophorus*	1749.94	/	3260.15	/	3260.15	/	3260.15	–
Bulwer's Pheasant	*Lophura bulweri*	1222.79	1796.73	/	1796.73	/	1796.73	/	+
Chestnut-bellied Partridge	*Arborophila javanica*	1078.77	350.00	714.33	273.71	714.40	458.41	714.34	–
Chestnut-headed Partridge	*Arborophila cambodiana*	779.49	/	578.62	/	578.62	/	578.62	+
Chestnut-necklaced Partridge	*Arborophila charltonii*	1118.35	203.75	1048.92	196.43	1048.92	165.00	1048.92	–
Chinese Francolin	*Francolinus pintadeanus*	349.61	128.68	72.63	132.03	234.18	127.92	219.08	–
Collared Brush-turkey	*Talegalla jobiensis*	47.25	/	66.60	/	66.60	/	66.60	–
Common Quail	*Coturnix coturnix*	87.62	340.38	/	340.38	/	340.38	/	+
Crested Argus	*Rheinardia nigrescens*	476.87	148.25	106.45	150.72	72.89	148.04	34.04	+
Crested Partridge	*Rollulus rouloul*	356.12	197.76	96.00	197.76	89.50	197.76	/	+
Crimson-headed Wood Partridge	*Haematortyx sanguiniceps*	1198.23	/	1285.78	/	1285.78	/	1285.78	–
Dusky Scrubfowl	*Megapodius freycinet*	127.71	/	124.88	/	124.88	/	124.88	+
Ferruginous Partridge	*Caloperdix oculeus*	164.47	132.67	436.05	131.20	409.15	134.38	416.75	–
Germain's Peacock-pheasant	*Polyplectron germaini*	421.32	173.42	/	173.42	/	173.42	/	–
Great Argus	*Argusianus argus*	1787.62	581.36	1593.82	616.51	1595.59	609.72	1612.99	–
Green Junglefowl	*Gallus varius*	495.93	345.80	/	347.60	/	347.66	546.03	–
Green Peafowl	*Pavo muticus*	948.73	1051.64	/	1051.64	/	1051.64	/	+
Green-legged Partridge	*Arborophila chloropus*	345.14	388.31	/	388.31	/	388.31	/	+
Grey Peacock-pheasant	*Polyplectron bicalcaratum*	287.98	/	351.73	/	351.73	/	351.73	–

(Continued)

TABLE 3 Continued

Species	Latin name	Current elevation	SSP126		SSP370		SSP585		Changes
			Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	Gain$_E$	Loss$_E$	
Grey-breasted Partridge	*Arborophila orientalis*	999.29	384.72	/	384.72	/	384.72	/	–
Hill Partridge	*Arborophila torqueola*	895.25	1015.71	580.93	962.80	580.03	/	581.25	+
Japanese Quail	*Coturnix japonica*	800.99	/	759.91	/	759.77	/	759.91	+
Kalij Pheasant	*Lophura leucomelanos*	101.78	149.19	205.27	85.97	203.09	67.87	202.57	–
Lady Amherst's Pheasant	*Chrysolophus amherstiae*	241.07	199.90	227.66	187.26	248.69	187.18	240.52	–
Long-billed Partridge	*Rhizothera longirostris*	517.30	/	465.18	/	465.18	/	465.18	+
Malay Crested Fireback	*Lophura rufa*	86.32	28.57	135.91	109.00	135.91	185.74	135.91	+
Malay Crestless Fireback	*Lophura erythrophthalma*	848.56	41.00	878.46	30.44	878.47	41.60	878.48	–
Malay Partridge	*Arborophila campbelli*	193.39	/	331.44	/	331.51	/	331.51	–
Malay Peacock-pheasant	*Polyplectron malacense*	400.48	456.13	357.60	418.91	357.39	417.26	357.45	+
Maleo	*Macrocephalon maleo*	164.20	/	444.55	/	444.55	/	444.55	–
Moluccan Scrubfowl	*Eulipoa wallacei*	365.65	/	366.53	/	366.53	/	366.53	+
Mountain Bamboo-partridge	*Bambusicola fytchii*	1170.31	/	759.98	/	759.98	/	759.98	+
Mountain Peacock-pheasant	*Polyplectron inopinatum*	243.57	/	293.55	/	293.55	/	293.55	–
Mrs Hume's Pheasant	*Syrmaticus humiae*	292.61	/	271.83	/	271.83	/	271.83	+
New Guinea Scrubfowl	*Megapodius decollatus*	230.40	388.03	/	388.03	/	388.03	310.02	+
Orange-footed Scrubfowl	*Megapodius reinwardt*	285.85	/	296.04	/	296.04	/	296.04	–
Orange-necked Partridge	*Arborophila davidi*	421.40	/	389.48	/	389.48	/	389.48	+
Palawan Peacock-pheasant	*Polyplectron napoleonis*	248.89	/	258.79	/	258.79	/	258.79	–
Philippine Scrubfowl	*Megapodius cumingii*	338.18	/	310.02	/	310.02	/	/	+
Rain Quail	*Coturnix coromandelica*	107.06	/	174.48	/	174.48	/	174.48	–
Red-billed Brush-turkey	*Talegalla cuvieri*	274.15	/	284.64	/	284.64	/	284.64	–
Red-billed Partridge	*Arborophila rubrirostris*	1345.21	/	1271.30	/	1271.30	/	1271.30	+
Rufous-throated Partridge	*Arborophila rufogularis*	1310.24	2935.67	/	2935.67	/	2935.67	/	+
Salvadori's Pheasant	*Lophura inornata*	289.99	/	359.11	/	359.11	/	359.11	–
Siamese Fireback	*Lophura diardi*	568.69	354.04	531.17	415.72	531.48	316.31	531.84	–
Silver Pheasant	*Lophura nycthemera*	213.95	253.41	/	253.41	/	253.41	/	+
Snow Mountain Quail	*Synoicus monorthonyx*	953.18	/	1028.41	/	1028.41	/	1028.41	–
Sula Scrubfowl	*Megapodius bernsteinii*	339.64	531.70	/	531.70	/	531.70	/	+
Tan-breasted Partridge	*Arborophila rolli*	425.32	99.36	400.22	96.48	371.57	87.69	408.86	–
Tanimbar Scrubfowl	*Megapodius tenimberensis*	55.53	/	67.81	/	67.81	/	67.81	–
Wattled Brush-turkey	*Aepypodius arfakianus*	1652.28	/	1652.28	/	1652.28	/	1652.28	/
White-cheeked Partridge	*Arborophila atrogularis*	328.52	342.38	/	342.38	/	342.38	/	+

PAs covered most areas with low diversity level under two dispersal scenarios (Figure 6). Conservation gaps for Galliformes species would mainly occur in areas with medium and high diversity levels under perfect dispersal scenarios (Figure 6A) and occur in areas with general, medium and high diversity levels under limited dispersal scenarios (Figure 6B).

4 Discussion

Our study emphasized that future climate and land-use changes would accelerate suitable habitat loss, and land use changes, Bio18, Bio13 and Bio2 were the main influencing variables. We found that precipitation of extreme quarters (Bio18 and Bio19) and

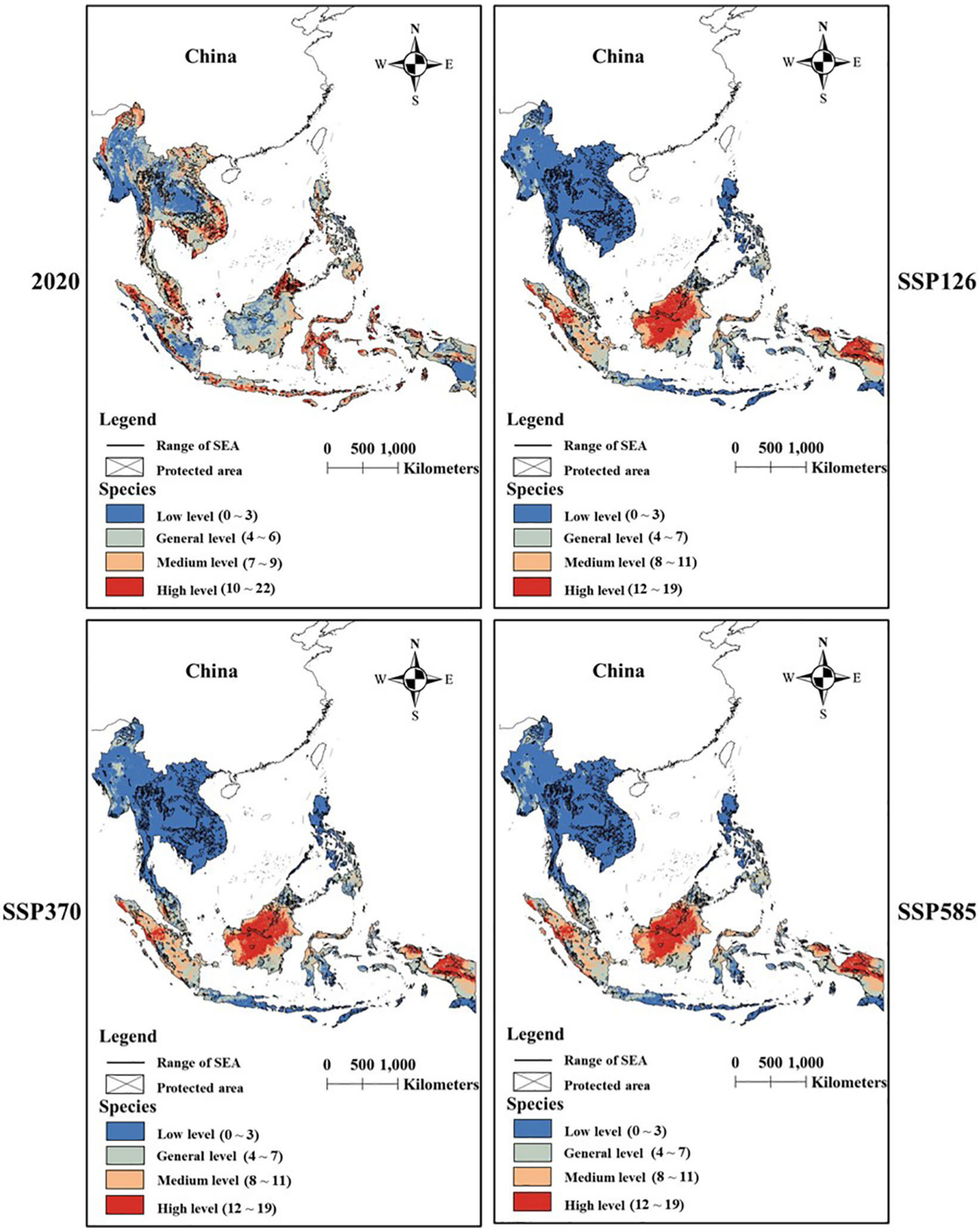

FIGURE 4
The difference in changes in species diversity between scenarios under perfect dispersal scenarios.

temperature (Bio2) explained a large proportion of variations in potential species distribution. Temperature and precipitation are widely recognized as the factors inducing suitable habitat loss (Conrey et al., 2016; Chiatante et al., 2021; Yao et al., 2021). Long-term changes can alter physiological conditions of species, thus affecting the climatic niche (Jiang et al., 2023) and forcing species to adjust their habitat selection strategies. Moreover, temperature and precipitation also affect life cycles and food resource distribution (insects and plants) (Memmott et al., 2007; Zi et al., 2023), which makes original habitats more suitable or unsuitable for species. Our model showed that precipitation had a stronger influence on the potential distribution of Galliformes species than temperature, probably because El Nino events have once caused severe drought in Southeast Asia. Precipitation shortage and severe drought are fatal to Galliformes species, as they not only impede the growth of plants but also cause disasters such as water scarcity and forest fires (Chokkalingam et al., 2005). Water and food resources are necessary for all animals to survive, and forest fires may directly kill Galliformes.

Our results showed that land-use changes had the biggest contribution to the potential distribution of Galliformes species, and forest cover would decrease and cropland area would increase

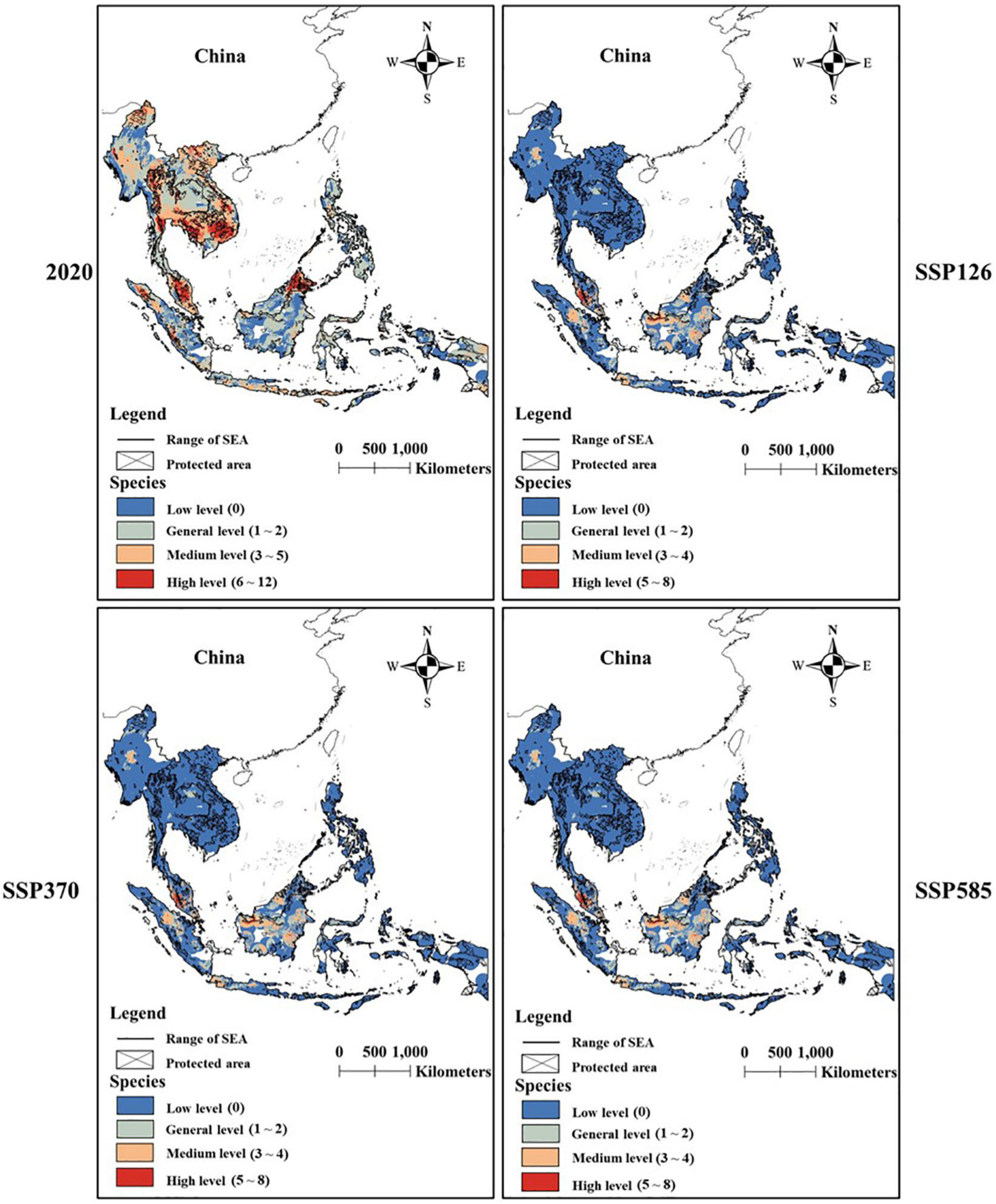

FIGURE 5
The difference in changes in species diversity between scenarios under limited dispersal scenarios.

by 2080. Many researchers have confirmed that the forests of SEA are disappearing, mainly due to deforestation and infrastructure construction (Savini et al., 2021; Reddiar and Osti, 2022). For instance, in order to earn a living, indigenous people of southern Palawan exploit and supply forest products and transform forest land into cropland (Smith and Dressler, 2019). Construction of roads has provided convenient access to forests for people in Indonesia (Wilkie et al., 2000). It is worth noting that hunting is rampant in SEA and Galliformes species are the main target of hunters (Gray et al., 2018; Savini et al., 2021). Therefore, convenient access to forests may increase the hunting risks of Galliformes species. Besides, land-use changes have absolutely increased the degree of forest fragmentation (Wilson et al., 2015; Tang et al., 2020). Although the suitable habitat area of 62 Galliformes species would increase or decrease, it is still a thorny issue whether species can move from original habitats to new habitats.

It is generally believed that future climate change will force species to move to higher elevations (LaSorte and Jetz, 2010; Freeman et al., 2018; Wallingford et al., 2020). Our results also supported this opinion, and showed that 22 (perfect dispersal scenarios) or 31 (limited dispersal scenarios) of 62 species would migrate upward under future scenarios, as climate and land-use changes would reduce the habitat suitability at lower elevations. For example, we predicted that Bornean Peacock-pheasant (*Polyplectron schleiermacheri*), Great Argus (*Rheinardia*

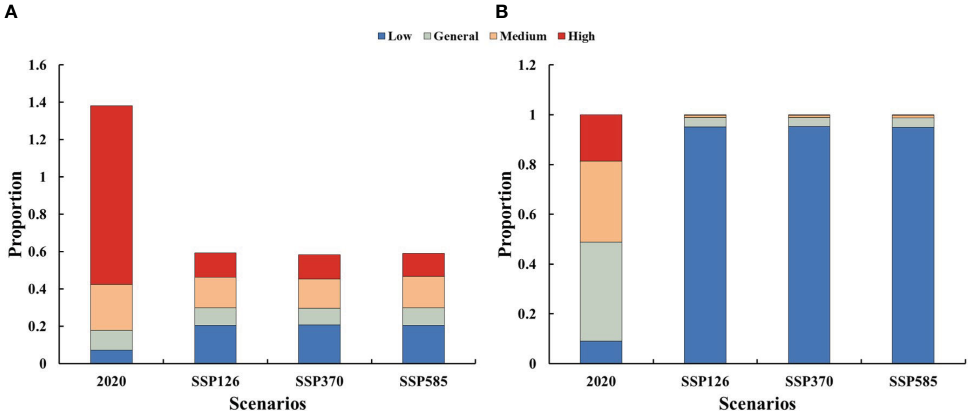

FIGURE 6
Protection proportion of suitable habitat with different diversity level under different scenarios. **(A)** Perfect dispersal scenarios; **(B)** Limited dispersal scenarios

ocellata) and Green Peafowl (*Pavo muticus*) will shift to higher elevation. According to IUCN red list, upper elevation limit of three species was 1000m, 1500m and 2100m, respectively. This indicated that changes in elevation of these three species meet the biological characteristics. However, these species may still be faced with survival stress if forest line has no changes. A recent study has demonstrated that the elevation of future habitats for 55 Galliformes species will increase or remain stable by 2100 in SEA (Namkhan et al., 2022). On the contrary, our results showed that 42 (perfect dispersal scenarios) or 30 (limtted dispersal scenarios) of 62 species would move to lower elevations or lose a large number of distribution areas at high elevations. There may be two explanations for this phenomenon. First, these species may have better adaptability to climate and land-use changes. Second, species living in warmer areas can tolerate future temperatures (the truncated niche hypothesis) (Feeley and Silman, 2010b), so they do not need to move to higher elevations. These species would choose to live at lower elevations, probably because of the deteriorating living conditions in original habitats caused by land-use changes.

Future climate and land-use changes would expand the area with low and high diversity of Galliformes species. As we expected, suitable habitat loss would expand the area with low diversity, but the expansion of areas with high diversity was inconsistent with our expectation. We believed that the finite suitable habitat would promote species aggregation under future changes. However, Galliformes species usually have similar habits and the restricted activity areas, which may cause a fierce competition between species. Our results also showed that these high-diversity areas were mainly distributed in Borneo, Sumatra Island, Palawan island and west New Guinea, and there was an obvious gap between these areas and protected areas. In addition, our model predicted that most species tended to be distributed at lower elevations under current and future scenarios (see Table 2). For instance, Japanese Quail (*Coturnix japonica*), White-cheeked Partridge (*Arborophila atrogularis*) and Orange-necked Partridge (*Arborophila davidi*) also utilized artificial habitat and lowland. As a result, there may be some conflicts between Galliformes and human at lower elevations. For instance, farming and forest product trade are developing rapidly on the southeast Palawan island, and numerous rice fields and commercial coconut gardens are widely distributed in lowland coastal plains of Borneo (Smith and Dressler, 2019). These human activities will have negative impacts on the survival of Galliformes. Moreover, island habitats will be the future suitable habitats for Galliformes, and these species are thought to have a limited dispersal ability between islands. Therefore, they will eventually be at risk of extinction if these areas are not effectively protected. Our findings suggested that it was necessary to establish more PAs or adjust the range of PAs based on the combined effect of climate and land-use changes, in order to conserve 30% of the planet by 2030 (also called 30 × 30) (Convention on Biological Diversity, 2022).

We acknowledged that SDMs are a simulation of species distribution, but we still believed SDMs are useful tools for predicting current and future species distributions (Araujo and New, 2007; Kindt, 2018; Dai et al., 2021), and may provide suggestions for managers to adjust conservation policies (Michalak et al., 2018; Prahalad et al., 2019; Tian et al., 2021). A previous study has pointed out that climate change may have limited impacts on altitudinal migrant species such as blood pheasant (*Ithaginis cruentus*) (Fan et al., 2020; Wallingford et al., 2020; IUCN, 2023). Unfortunately, we set buffers to limit the dispersal of Galliformes, but we did not take into account species migration in this study. Although previous studies have assessed the independent effects of climate change and habitat loss on Galliformes in SEA (Savini et al., 2021; Namkhan et al., 2022), our study demonstrated that it was necessary to consider the combined impacts of both factors on Galliformes. We did not directly compare the impact of climate and land-use changes, as this was not the purpose of our study. Taken together, land-use change had a stronger impact than climate change due to its immediacy and irreversibility, but we acknowledged that the long-term effect of climate change could not be ignored. Hopefully, our results will be used as a basis for understanding the future distribution of Galliformes species in SEA and provide scientific guidance for biodiversity conservation in the future.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The studies involving humans were approved by the Institutional Review Board of the National Center for Health Statistics. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

ZL and JX designed the study. ZL, ST, and SL developed the methods. ZL, ZZ, and LA collected the data. ZL, ZZ, YP, and XL conducted the analyses. JL, YW, and JX reviewed and edited the paper. ZL and JX wrote the paper. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1216769/full#supplementary-material

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Biodiversity conservation and ecological value of protected areas: a review of current situation and future prospects

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The establishment of protected areas (PAs) is an effective way to biodiversity conservation while maintaining the multiple functions of ecosystem services. However, there is still a lack of comprehensive analysis on the relationship between PAs, biodiversity conservation, and ecological value in the field of research on prospects. Therefore, based on the research progress of literature content, this paper systematically reviews and evaluates domestic and international studies in terms of the biodiversity conservation and the ecological value of PAs. The results showed that relevant studies in recent years have mainly analyzed the spatial layout, area changes and conservation effectiveness of PAs in relation to biodiversity; By constructing the connotation system of ecological value concept of PAs, the research progress of ecological value accounting, ecological value realization and transformation, and ecological value types of PAs is further discussed, and the prospects of biodiversity conservation and ecological value research of PAs is proposed. This study provides a reference for the implementation of the Kunming-Montreal Global Biodiversity Framework and the construction and optimization of PAs system.

KEYWORDS

protected areas, biodiversity conservation, ecological value, key biodiversity areas, human well-being

1 Introduction

Biodiversity is related to human well-being and is an important foundation for human survival and development. The establishment of PAs is an effective way to biodiversity conservation while maintaining the multiple functions of ecosystem services. Addressing climate change and biodiversity conservation are two global hotspots and difficult environmental issues. Advancing synergies between climate change response and biodiversity conservation is critical to addressing the current environmental crisis. PAs are specific spatial areas whose main function is to protect ecosystems, and they play an important role in biodiversity conservation, maintaining the stability of ecosystems and improving the quality of the ecological environment, as well as playing a primary role in maintaining national ecological security (Leverington et al., 2010; McDonald and Boucher, 2011).

As an area designated and managed by countries around the world to effectively protect biodiversity (Borrini-Feyerabend et al., 2013), PAs are one of the most effective ways to protect natural resources and ecological environment. As defined by the International Union for Conservation of Nature (IUCN), a protected area is: “A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Dudley, 2016). According to the classification criteria of the IUCN, PAs can be divided into six categories: strict nature reserve and wilderness area, national park, natural monument or feature, habitat/species management area, protected landscape/seascape, protected area with sustainable use of natural resources. PAs not only provide a large amount of raw materials for human beings, but also have great ecological and economic benefits (Mulongoy and Badu, 2008). The ecological value assessment of PAs has been paid more and more attention, and has become a frontier topic in ecology and environmental economics (Figgis et al., 2015).

Although the concept of PAs is currently defined differently by countries and international organizations around the world, the conservation goals basically cover biodiversity, typical ecosystems and important natural resources. With the development and implementation of the post-2020 global biodiversity framework, research in the field of biodiversity conservation in PAs has also been deepened. The research focuses on key ecosystems and rare and endangered species, their status and changes, and a series of scientific issues such as the number and area of PAs, the number of important ecosystems and species protected, and the effectiveness of biodiversity conservation. The ecological value of PAs is one of the bases for classification and grading of the new PAs system. According to the framework proposed by the IUCN’s Wilderness Protected Areas: Management Guidelines for IUCN Category 1b Protected Areas, PAs such as wilderness have instrument value and instinct value, which is essential for protecting biodiversity and maintaining ecosystem services, while helping to maintain cultural and linguistic diversity (Casson et al., 2016). The research of ecological value of PAs is of key significance for promoting the construction and development of new PAs system and deepening the realization of the value of ecological products.

However, there is a lack of systematic analysis and interpretation of hot topics in biodiversity conservation and ecological value research in PAs, which makes it difficult to predict their potential hot spots and research trends. This paper aims to systematically review the main progress of biodiversity conservation research in PAs in the past 20 years, explore the research hotspots and trends in the field of ecological value of PAs, and put forward prospects for the future development direction, so as to promote the in-depth development of related research on PAs, with a view to providing reference for the formulation and implementation of the Kunming-Montreal Global Biodiversity Framework, especially in the construction and optimization of PAs systems.

2 Methods

In order to systematically and comprehensively review the research status of PAs, CNKI (China National Knowledge Infrastructure) and WoS (Web of Science) literature databases were used as data sources, and the search was conducted with the subject terms and titles “protected areas, biodiversity conservation and ecological value”. To ensure the comprehensiveness of the data sources, “national park”, “nature reserve”, “nature park”, “scenic area”, “natural heritage site”, “wetland park” and “forest park” were used to replace the PAs for secondary retrieval; ecological products value, natural capital value, ecosystem service value, ecological capital value, ecosystem assets value, and ecosystem assets value, were used to replace ecological value for re-retrieval. The literature types were defined as articles and review, with a time span of 2003–2022, and the retrieval time was April 2023. All 2,164 documents were de-duplicated in CiteSpace 5.8.R2, and 1,051 valid search results were retained.

After processing and analyzing the literature with the software CiteSpace 5.8.R1, the COOC 9.94 software was used to perform word frequency statistics on the retained valid literature data and determine the high-frequency words, and co-word cluster analysis was used to construct the co-word matrix. Then, high-frequency keywords were clustered in VOSviewer 1.6.16 to realize multi-dimensional quantification and visualization of literature data, identify research hotspots of biodiversity conservation and ecological value in PAs, describe the interaction between research hotspots and the closeness of the internal correlation in the research field, and judge their status and research development.

3 Results

The keywords in the literature were processed with the help of COOC software, and the retained effective keywords were counted. The results showed that the keywords with high frequency were: nature reserves, ecosystem services, biodiversity conservation, etc. (Table 1). In order to improve the credibility of the study, the samples were selected as keywords with a frequency of 10 times or more for subsequent analysis.

3.1 The quantity and spatial distribution of PAs

How many PAs need to be built globally to effectively conserve sufficient biodiversity has always been a key issue of concern for scholars around the world (Baillie and Zhang, 2018). The 2010 target for PAs adopted by the 7th Conference of the Parties to the Convention on Biological Diversity includes the goal of “effectively protecting at least 10% of each ecoregion in the world” (Coad et al., 2009). In recent years, many scholars have proposed the goal that nature reserves and PAs should cover 30% of the world’s land,

TABLE 1 Complete co-occurrence matrix of top 10 high-frequency keywords.

	protected areas	ecosystem service	biodiversity conservation	marine protection area	ecological value	climate change	sustainable development	key biodiversity areas	human well-being	social-ecosystem
protected areas	146	52	34	6	37	18	26	41	24	15
ecosystem service	52	135	27	19	13	16	9	12	8	7
biodiversity conservation	34	27	120	5	34	13	11	7	9	4
marine protection area	6	19	5	114	16	6	2	3	7	8
ecological value	37	13	34	16	106	8	9	4	6	3
climate change	18	16	13	6	8	92	3	5	5	4
sustainable development	26	9	11	2	9	3	71	3	1	9
key biodiversity areas	41	12	7	3	4	5	3	68	2	5
human well-being	24	8	9	7	6	5	1	2	57	1
social-ecosystem	15	7	4	8	3	4	9	5	1	54

freshwater and oceans by 2030 (Dinerstein et al., 2019). In order to reverse the continuous decline of biodiversity and ensure the sustainable development of human society, scholars from various countries have also paid more attention to PAs. At the 9th World Wilderness Congress in 2009, Harvey Locke proposed that at least 50% of the area should be set aside as PAs or OECMs (Other Effective Area-based Conservation Measures) at the global scale (Cao et al., 2019). Scientists have also called for 50% of terrestrial and marine areas to be set up as some form of PAs or OECMs, and estimate that these areas could protect 85% of species from extinction (Wilson, 2016).

Biodiversity is not evenly distributed on the earth, and it is necessary to find the most concentration areas of biodiversity for priority conservation, and on this basis balance the economic, social and ecological benefits, so as to achieve the optimal spatial layout of PAs. By identifying important areas of biodiversity such as biodiversity hotspots and key biodiversity areas (KBAs), the key question of "where to conserve" can be further answered. The identification, ranking and vacancy analysis of KBAs can provide an important basis for the expansion of PAs networks (Langhammer et al., 2007), and become an important means to assess the progress of global biodiversity targets. Recent studies have shown that approximately 55.8% of global KBAs have been covered by PAs. When further designating 0.36% of the terrestrial area within the global KBAs into PAs, the conservation coverage of threatened vertebrates can be increased by an average of approximately 14.7% (Kullberg et al., 2019). Determining whether the location and scope of the current PAs is reasonable, and making boundary and location adjustments are essential for effective conservation. For areas affected by long-term human impacts, it is necessary to take advantage of the relationship between communities and nature in different regions to promote sustainable resource utilization and new models of PAs, and to expand the area of PAs based on the existing ones.

3.2 Biodiversity changes and influencing factors in PAs

As one of the core areas of biodiversity conservation, whether PAs can effectively protect the ecosystem and wildlife in the region, i.e., the study of the effectiveness of PAs and its influencing factors, is also a key scientific issue in the field of PAs (Figure 1).

Despite the increasing impacts of climate change and human disturbances on biodiversity, changes in land cover/use and landscape patterns within PAs are generally less than outside PAs (Nagendra, 2008; Rodriguez-Rodriguez et al., 2019), reflecting the stability of PAs in response to external disturbances. Studies around changes in forest and wetland ecosystems are relatively more numerous than those in grassland, desert and marine ecosystems in PAs (Xin et al., 2014; Song et al., 2018). From the perspective of species, scholars in various countries have conducted systematic monitoring of rare and endangered species or flagship species under key protection in PAs. A large number of biodiversity monitoring networks and field stations have been established, and the changes of biodiversity are measured by quantitative monitoring data of ecosystems and species in the field (Geldmann et al., 2021).

The conservation effectiveness of PAs is also one of the research hotspots, and scholars have conducted numerous studies at the global scale, national scale, and individual PAs. The biodiversity change or conservation effectiveness of PAs is affected by a combination of factors such as climate change, human disturbance and related policies. Climate change leads to the continuous migration of some species in search of new suitable

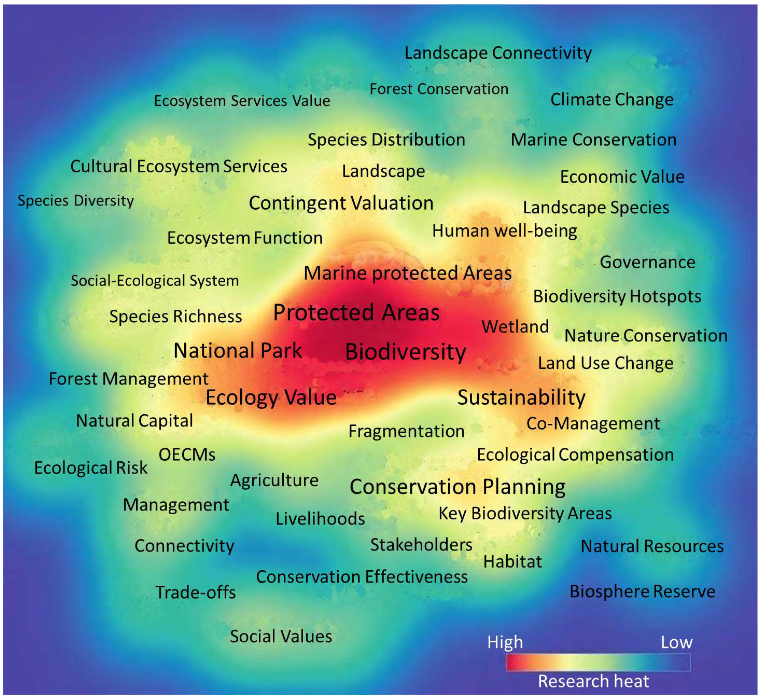

FIGURE 1
Heat map of study distribution.

habitats, and some species even migrate to habitats outside the PAs, resulting in the disappearance of these species within PAs, which will not be conducive to the effective conservation of these species (Klausmeyer and Shaw, 2009; D'Amen et al., 2011). Although the establishment of PAs has mitigated the impact of human disturbance to a certain extent (Guette et al., 2018; Feng et al., 2022), however, a global study still shows that the average degree of human disturbance in some PAs is significantly higher than that outside (Geldmann et al., 2021). The increase of human disturbance has a significant impact on the effectiveness of PAs in protecting ecosystems (Feng et al., 2022) or species (such as giant pandas, Wei et al., 2020). In addition, the human disturbances in the surrounding areas of PAs may be significantly increased due to the existence of PAs. This phenomenon is called the "leakage effect" of PAs, which is not conducive to the overall protection of PAs (Ewers and Rodrigues, 2008). National policy is also an important factor. Recent studies have also focused on the impact of PAs downgrading, downsizing, and degazettement (PADDD) events on the conservation effectiveness (Qin et al, 2019).

3.3 Comprehensive assessment of ecological value of protected areas

The ecological value assessment of PAs is responsible for various tasks such as maintaining ecological sustainability, ensuring equitable distribution of resources, and achieving human well-being (Liu et al., 2010), and the current international ecological value assessment system of PAs mainly covers ecosystem services value (ESV) and ecosystem intrinsic value (EIV).

Ecosystem services are the benefits directly or indirectly obtained by human beings from the ecosystem (Costanza et al., 1997). PAs are the key sources of ecosystem services, and its value assessment is an indispensable step to balance protection and development. At the scale of PAs, the main research contents include comprehensive evaluation and dynamic change of ecosystem service value of PAs (Považan et al., 2015), single ecosystem service value assessment of PAs (Belkayali et al., 2010), and single ecosystem service value assessment of multiple PAs at a specific spatial scale (Mayer and Woltering, 2018) The evaluation methods mainly include two types: monetized valuation and non-monetized valuation. The former includes revealed preference method, stated preference method and cost method, and the latter includes ranking method (Farber et al., 2006). Relatively, the connotation system and evaluation method of the ecosystem intrinsic value are not yet mature and are rarely applied in PAs. However, scholars gradually realize the importance of distinguishing the ecosystem intrinsic value and try to interpret the connotation of the ecosystem intrinsic value, and also believe that the assessment of ecosystem intrinsic value can provide a basis for sustainable management decisions in PAs (Sheng et al., 2019).

The analysis of the interest relationship in the realization of ecological value of PAs is also one of the research hotspots. To achieve the conservation goals of PAs, it is necessary to formulate effective authorization governance and adaptive management plans, and stakeholder participation is an important link. In the study of the influencing factors of ecological value, previous studies have verified the factors that may cause the change of ecological value in monetary valuation or non-monetary valuation, and explored the elastic response mechanism of ecosystem service value to the influencing factors. These factors mainly include: (i) land use type changes, such as arable land expansion and grassland degradation (Shi et al., 2020); (ii) species invasion and biomass changes in PAs (Turpie et al., 2003; Grilli et al., 2017); and (iii) human activity disturbance, indigenous characteristics and public perception (Martín-López et al., 2007; Kenter et al., 2016; Riper et al., 2017).

The ecological value of PAs can promote human well-being. PAs can provide humans with intangible ecological values such as aesthetics, recreation and cultural heritage (Vejre et al., 2010). Human well-being has multiple components, including the basic material conditions needed to maintain a high quality of life, the right to freedom and choice, health, good social relations, and security. Related studies include two main aspects: (i) the impact and assessment of the establishment of PAs on human well-being changes, where negative impacts can be balanced by positive impacts under specific external conditions (Gjertsen, 2005; Pullin et al., 2013; Naidoo et al., 2019), but the discussion on how to achieve this situation needs to be expanded; (ii) The relationship between ecosystem services and human well-being and how to ensure equal access to ecosystem services, such as the role of payment for ecosystem services in poverty reduction, and the impact relationship between increased ecosystem resilience and human well-being promotion (Daw et al., 2011; Daw et al., 2016).

4 Conclusions and future directions

4.1 Conclusion

In order to maintain biodiversity and ensure the stability of ecosystem function, this paper summarizes and reviews the relevant researches in recent years from the aspects of spatial layout of PAs, the relationship with biodiversity distribution, and the change of biodiversity in PAs. The existing research mainly focuses on the state of PAs and biodiversity at a certain stage, and is devoted to exploring a series of key scientific issues such as the number and spatial distribution of PAs. At the same time, the biodiversity in PAs will undergo temporal and spatial dynamic change with climate change, human activities and their own succession, etc. Based on the analysis of biodiversity changes in PAs, a large number of conservation effectiveness assessment studies have been conducted to identify the main influencing factors of different PAs. Ecological value assessment and accounting of PAs is the current core mainstream research hotspot, focusing on the value assessment of ecosystem services provided by PAs to humans, and gradually forming a methodological system, but there is still much room for development in the intrinsic value assessment. The research on the interest relationship of ecological value realization of PAs focuses on the implementation of policies such as eco-industry development and ecological compensation in PAs, as well as the demands and responses of stakeholders in the process of ecological value management. The existing research system on the influencing factors of ecological value of PAs, ecological value and human well-being promotion research needs to be further improved, and further development can be achieved by enhancing the association with mainstream research hotspots in the future.

4.2 Future directions

Studies have shown that focusing solely on the goal of the area, quantity and proportion of PAs, while ignoring the changes in biodiversity, makes it difficult for many PAs to achieve effective protection (di Minin and Toivonen, 2015). Future research should pay more attention to the comprehensive role of PAs in biodiversity conservation, maintaining ecosystem services and carbon sequestration capacity, effectively plan the spatial layout of PAs, and predict potential important areas in combination with future trend changes. Combined with the analysis of the dynamic changes of long-term monitoring data of various indicators, the systematic evaluation of the effectiveness of PAs can be realized. The research results of spatial optimization layout, protection effectiveness evaluation and major conservation objects changes of PAs are integrated to identify and clarify the areas of new PAs and planned corridors, and effectively improve the quality and connectivity of PAs. By combining the PAs with the sustainable development of the areas where they are located, it is further explored how to promote the sustainable development model of human–earth harmony in and around the PAs on the premise of improving or maintaining the protection effectiveness of the PAs.

The establishment of ecological value assessment system applicable to the scale of PAs can carry out comprehensive ecological value assessment practice in different types of PAs, and enrich the research perspective of ecological value realization of PAs. For different types of PAs, comparative and applicability studies on ecological value realization models of PAs to help develop ecological product markets; Construct a stakeholder system for the realization mechanism of ecological value of PAs, explore a benign interaction mechanism between human well-being promotion and ecological value transformation, provide theoretical support for the construction of ecological compensation system and governance optimization of PAs, and promote the sustainable transformation of ecological value of PAs. Strengthen the application research on the influencing factors of ecological value, explore the influencing factors of economy, policy and ecology, carry out validation and comparative studies, provide the basis for the formulation of resource management and utilization policies of PAs, and improve the protection efficiency.

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

Author contributions

HW: Funding acquisition, Investigation, Methodology, Writing – review & editing. XH: Conceptualization, Data curation, Formal Analysis, Software, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Vacancy analysis and layout optimization of Changdao natural protected area from the perspective of multi-objective collaboration

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Research on vacancy analysis and spatial layout of protected natural areas has been carried out for many years around the world, but most of the research objects are land-type protected natural areas, while studies on Marine protected natural areas are relatively rare, and there are few cases to carry out integrated optimization research on spatial layout of protected natural areas. This study will take Changdao in Yantai, Shandong Province, China as an example, from the protection of how much? How representative? Where is it protected? Starting from the three problems, the vacancy analysis is carried out, and the integrated optimization research is carried out based on the existing spatial layout, aiming at the rescue protection, coordinated protection and forward-looking protection. The results show that the integrated and optimized Changdao protected area eliminates the protection vacancy, integrates the overlapping protected areas, optimizes the unreasonable protected space, alleviates the contradiction between protection and development, promotes the coordinated development of ecology and economy and society, and can provide a scientific reference for the integrated and optimized spatial layout of Marine protected areas.

KEYWORDS

marine, natural protected area, integration, optimization, spatial arrangement

1 Introduction

In recent years, under the combined impact of global climate change intensifying human activities, the ecological effects of unhealthy succession of natural ecosystems have negatively affected the quality of human life. It is therefore imperative to implement complete protection of natural ecosystems. Identifying a natural protected areas on a scientific basis would help prevent the disorderly expansion of human exploitation (McNeill, 1994; Montesino Pouzols et al., 2014; Tittensor et al., 2019). China has established a system of natural protected areas mainly comprising of national parks in an aim to protect biodiversity, preserve natural heritage, improve ecological environment quality, and strengthen national ecological security. At the same time, these natural protected areas collectively play a key role in the supply of high-quality ecological products and the provision of public services such as science, education and recreation to the whole society (General Offices of the CPC Central Committee and The State Council, 2019; Tang et al., 2019; Tang et al., 2020). As the core area of marine protected areas (Hamid et al., 2021), islands sustain a mixed terrestrial and marine ecosystems (Shi et al., 2009), playing a basic role in maintaining biodiversity (Correia et al., 2021), regulating the productivity and material cycle of the island ecosystem, and are of high conservation value (Tilman et al., 1997; Hooper et al., 2004; Cardinale et al., 2006; Wei et al., 2008). Previous works on spatial layout of natural protected areas, however, are problematic (e.g. some biologic species together with their habitats were not included) due to the lack of scientific evidence.

The analysis of protected areas in both terrestrial and marine ecosystems (forests (Wang et al., 2010; Huang et al., 2014; Wang et al., 2018; Zhang, 2022), wetland (Wang et al., 2010; Huang et al., 2014; Wang et al., 2018; Zhang, 2022; Hong et al., 2023), desert (Lu et al., 2019), grassland (Liu et al., 2014), etc.), has been intensively studied over the past several decades (Huang et al., 2022). The protected areas in islands, however, have been rarely studied. Moreover, most of the existing studies are policy-oriented guidance, instead of detailed optimization scheme for spatial layout. China is promoting the integration and optimization of protected natural areas across the country, and relevant studies have emerged, mainly covering: (1) classification system and selection index system of protected areas (Gao et al., 2019; Hou et al., 2019; Ma et al., 2019; Qu et al., 2019; Tang et al., 2019; Chen and Jiao, 2020; Li et al., 2020; Ouyang et al., 2020; Tang et al., 2020a; Zhao et al., 2020); (2) basic ecological theory of integrated optimization of protected areas (Tang and Luan, 2017; He and Su, 2019; Lin and Zhou, 2019; Jiang et al., 2021; Tang, 2021); (3) rules and procedures of integrated optimization (Ma et al., 2019; Qu et al., 2019; Huang et al., 2020; Li et al., 2020; Tang et al., 2020b; Gao et al., 2021; Liu et al., 2022);and (4) practice of integrated optimization (Shang and Wang, 2019; Liu et al., 2020; Liu et al., 2021; Luo et al., 2021; Weng et al., 2021; Zeng et al., 2021). Two shortcomings exis: (1) marine protected areas are less studied, in comparison with those on land. The boundaries of landscape units, such as mountains and forests, within the terrestrial ecosystem are clearly defined. In order to establish protected areas, the outer edge line of each landscape unit can be directly adopted. Comparing with those in island protected areas where most of the landscapes and protected items are under sea level.In order to facilitate the management and positioning of boundary point buoys, the outer boundary of the island protected area is predominantly linear. Some of the protected marine animals have long-distance migrating pathways, making it difficult to protect the whole area. Due to the inherent differences between marine and terrestrial ecosystems, the vacancy analysis and layout optimization methods of land-type protected areas may not be applicable to island protected areas; (2) There has been limited connection between vacancy analysis and layout optimization studies.

In this study, we conducted vacancy analysis to natural protected areas in the Changdao Island on three issues (Zhang and Sun, 2019): "how many species are protected", "representativeness of the protected species" and "which areas should be protected". We further optimize the existing spatial layout of protected areas by combining protection objectives at different levels, with a view to building an integrated optimization rule system applicable to protected areas on islands (Figure 1). Our results can provide new guidance for the integration and optimization of national marine protected areas.

2 Study area profile

Located between Liaodong Peninsula and Jiaodong Peninsula, the Changdao Island chain consists of 151 islands, spanning over 56.41 km from south to north and 30.81 km from east to west. The

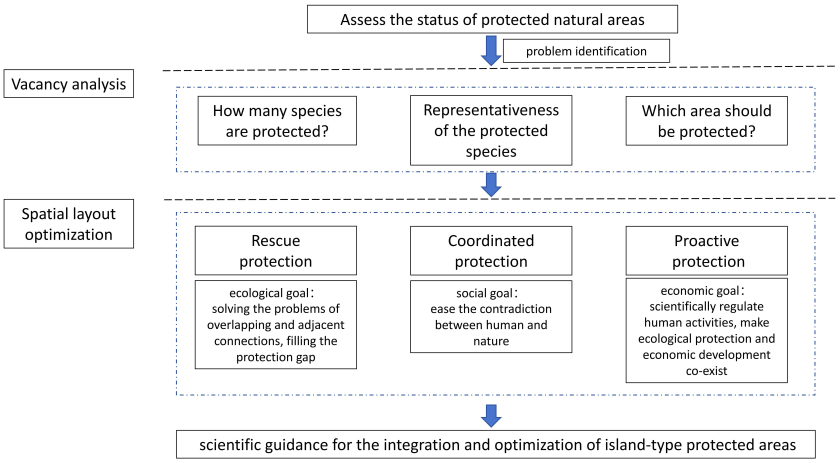

FIGURE 1
Overall research strategy schematic.

total administrative area of Changdao Island is 3,301.97 km^2, including a land area of 59.25 km^2 and a sea area 3,242.71 km^2 (Figure 2). The Changdao Island chain is located on the East Asia-Australasia international bird migration route, providing a valuable resting place for migratory birds and migratory animals such as harbor seals and East Asian finless porpoises, This area therefore serves as a key "pump station" for the ecosystems in the Yellow Sea and Bohai Sea. The ecological importance of this area leads to the establishment of 9 different types of natural protected area (Figure 3; Table 1). However, there is a massive overlap in spatial layout among the 9 protected areas. For instance, one protected area was repeatedly claimed by the other 5 protected area (Wang et al., 2019). The sum of approved area of each protected area is 2,472.96 km^2, far exceeding its actual protected area is 1,894.65 km^2.

3 Analysis of vacancies in protected area

3.1 How many species are protected?

The Changdao Island chain is biological diverse. During the observation from May 2019 to October 2021, up to 3,543 biological species were found, including 1,541 species of plants and 2002 species of animals. Although there are many protected areas in this area, only the national nature reserve has been scientifically investigated. According to the historical statistics (listed in Table 2), most of the animals on land (excluding birds), birds, and marine animals discovered in Changdao have been protected by the Changdao National Nature Reserve, but less than half of the plant species have been protected, creating an apparent protection vacancy. This is possibly because the field investigation in 2016 had a small spatial coverage of the whole area. If all the existing protected areas are integrated as one in the future, it is necessary to update the protection list based on the latest scientific data and fill the protection vacancy. In addition, Changdao has abundant geological and cultural landscapes (Table 3) that have been formally protected.

3.2 Representativeness of the protected species

According to the latest "National Key Protected Wildlife List" issued in 2021, a total of 96 species of wildlife under national key protection have been found in Changdao, including 90 species of birds and 6 species of marine animals. Among these 90 species of birds, there are: (1) 21 Class I national key protected species

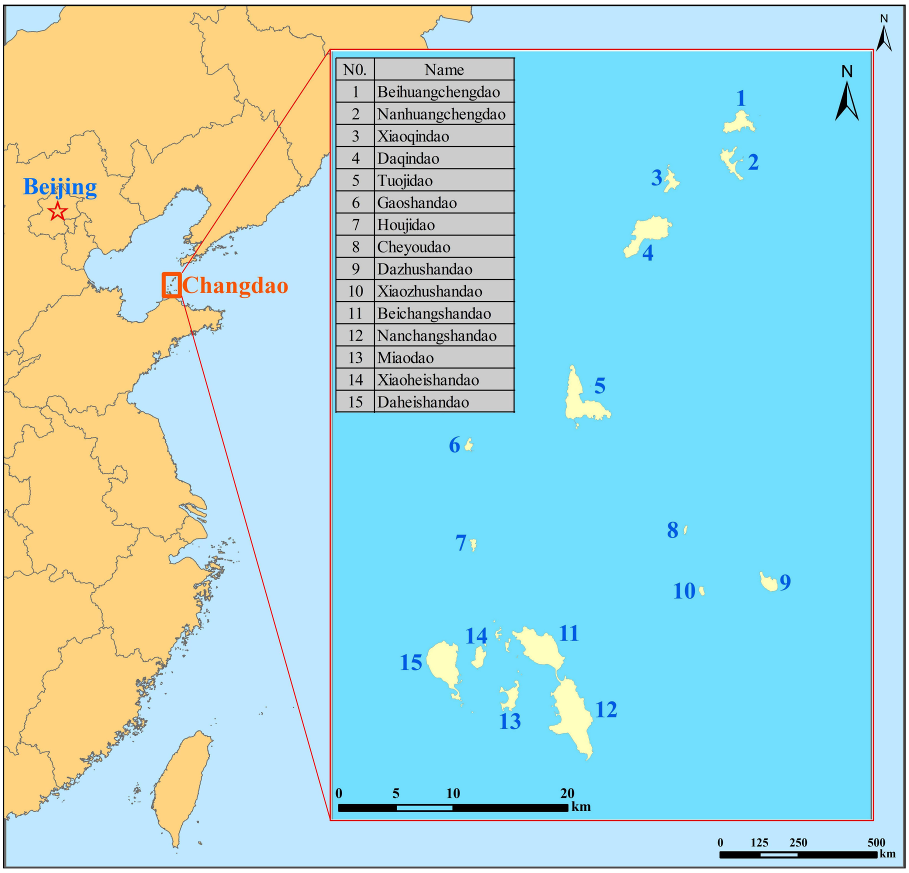

FIGURE 2
Changdao location.

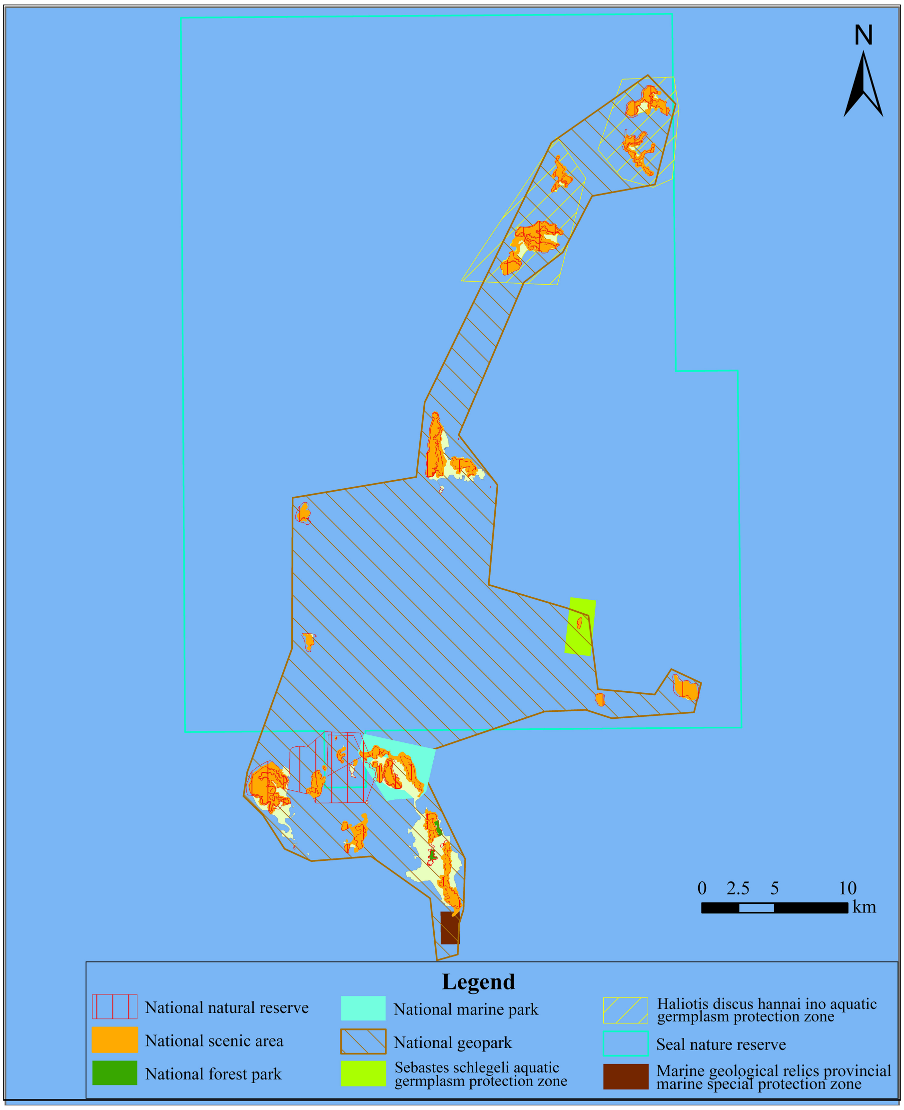

FIGURE 3
Spatial distribution of Changdao natural protected areas.

including *Aythya baeri*, *Mergus squamatus*, *Otis tarda*, *Grus leucogeranus*, *Grus japonensis*, *Saundersilarus saundersi*, *Phoebastria albatrus*, *Ciconia nigra*, *Ciconia boyciana*, *Platalea minor*, *Egretta eulophotes*, *Aegypius monachus*, *Clanga clanga*, *Aquila nipalensis*, *Aquila heliaca*, *Aquila chrysaetos*, *Haliaeetus albicilla*, *Falco cherrug*, *Emberiza aureola*, *Grus vipio*, *Grus monacha*; (2) Class II national key protected 69 species, including *Anser albifrons*, *Cygnus olor*, *Cygnus columbianus*, *Cygnus cygnus*, *Aix galericulata*, *Podiceps auratus* and etc. Among the marine animals under national key protection, there are two Class I national protected species, namely *Phoca largha*, Western Pacific harbor seal, and *Balaenoptera acutorostrata*, minke whale. Class II national protected species: include East Asian finless porpoises (*Neophocaena sunameri*), killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), and North Sea lions (*Eumetopias jubatus*). In addition, a considerable number of *Gloydius changdaoensis*, a vulnerable species on the IUCN Red List of Endangered Species, has been found in the the Changdao Island chain. There are also some native populations of sea curiotica found in this area, such as *Haliotis discus hannai Ino*, *Strongylocentrotus nudus*, *Stichopus japonicus*, Besides, it is also an important habitat for important economic fish such as *Sebastes schlegelii*. According to the latest List of Key Protected Wild Plants issued in 2021, excluding cultivated plants, there are three species of wild vascular plants under national Class II protection namely *Zoysia sinica*, *Glycine soja* and *Glehnia littoralis*. In addition, several geologically and historically important landscapes are located in this area, including the sandbank that separates the Yellow Sea and Bohai Sea, the rarely-found island loess, coastline progradation and retreat, ancient societal relics and Mazu culture. According to the

TABLE 1 Information of Changdao natural protected areas.

	Name	Area (hm^2)	Main protected object
1	National natural reserve	5591.0	Eagles, falcons and other birds of prey
2	National scenic area	3542.0	Geological and geomorphic landscape (marine erosion and accumulation) Human landscape(Northern Mazu culture, Beizhuang ruins)
3	National geological park	54640.0	Geological geomorphology and geological structure landscape(marine erosion and accumulation, volcanic, geological hazard of collapse, island loess, natural stone painting, colored sphaerite) Ancient human cultural ruins
4	National forest park	5700.0	Forest vegetation, birds, snakes and other wildlife resources and other landscapes
5	National Marine park	1126.47	Pristine natural shoreline, Harbor seals and their important habitats, Jiuzhangya sea erosion landform, Crescent Bay pebble Beach
6	Haliotis discus hannai ino and strongylocentrotus nudus national aquatic germplasm resources reserve	2600.0	Haliotis discus hannai ino, Strongylocentrotus nudus, Stichopus japonicus and their key habitats
7	Sebastes schlegeli national aquatic germplasm resources reserve	700.0	Sebastes schlegeli and their key habitats
8	Provincial seal nature reserve	173100.0	Harbor seals and their important habitats
9	Changshanwei provincial marine geological heritage reserve	297.0	Changshanwei marine geological resources and marine ecological resources

main objectives of the existing protected areas, most birds, choice rare sea food, important economic fish, land animals, plants, geological heritage landscape and cultural landscape with important protection value have been included in the protection list, but among the marine animals under key national protection, only the Western Pacific harbor seal has been included in this list. Minke whales, East Asian finless porpoises, killer whales, false killer whales, and North Sea lions are still unprotected.

3.3 Which area should be protected?

As shown in Figure 2, long-distance migratory species such as birds and harbor seals, key protected plants, and coastal erosion landscapes are distributed in each island and its surrounding waters. The main protection areas for the native populations of sea treasures such as sea cucumber are Daqin Island, Xiaoqin Island, South Huangcheng Island and North Huangcheng Island. The protection area of the Sebastes is located in Cheyou Island. The main protection areas of Miaodao Gloydius are located in Nanchangshan Island, Beichangshan Island, Daheishan Island, Xiaoheishan Island and Miaodao Island. The boundary sandbank separating the Yellow Sea and Bohai Sea is located at the tail of Changshan Mountain in the south of Nanchangshan Island. The loess is mainly distributed in Daheishan Island and Tuoji Island. Beizhuang site is located on Daheishan Island; The main protection area of Mazu culture is located on the Miao Island.

At present, minke whales, East Asian finless porpoises, killer whales, pseudo-killer whales, and northern sea lions are still unprotected, and their living domains remain unclear. Surveys performed from 2019 to 2020 reveal that the East Asian finless porpoise appeared mainly in the waters to the east and west of the Changdao Island chain, demonstrating that there is still a total area of 575 km^2 uncovered by the existing protected areas. The living domains of Minke whales, orcas, pseudo-orcas, and Beihai lions remain poorly determined. Existing evidence only comes from fisherman’s occasional witness. For example, minke whales have appeared in the northern waters of Beichangshan Island, orcas appeared in the northern waters of Beichang Island and the eastern waters of Tuoji Island, pseudo-orcas appeared in the eastern waters of Changdao Island, and Beihai lions appeared in the waters around Daqin Island and Nanhuangcheng Island.

TABLE 2 Changdao scientific survey data over the years.

Time			2016	2019~2021	Proportion
Scope			National natural reserve	Changdao	
Species Number	botany		730	1541	47%
	Animal	Land animals (excluding birds)	675	790	85%
		Birds	330	346	95%
		Marine animal	650	866	75%

TABLE 3 Conservation status of representative species and landscapes.

Representative protected target				Species/ Landscape	Protection State	Protected Area	Vacancy
Important species	animal	Birds		90	90	National natural reserve National forest park	\
		marine animal	national key protected species	6	1	National marine park Provincial seal nature reserve	5
			choice rare sea food	3	3	Haliotis discus hannai ino and strongylocentrotus nudus national aquatic	\
			Economically fish	1	1	Sebastes schlegeli national aquatic germplasm resources reserve	\
		terrestrial animal		1	1	National forest park	\
	botany			3	3	National natural reserve National forest park	\
Representative landscape	Geological heritage landscape			Yellow Bohai Sea boundary bar	√	National scenic area National geological park Changshanwei provincial marine geological heritage reserve	\
				Island loess	√	National geological park	\
				Marine deposition and erosion landscape	√	National scenic area National geological park National marine park	\
	human landscape			Beizhuang ruins	√	National scenic area	\
				Mazu culture	√	National scenic area	\

4 Optimization of protected area's spatial layout

In this study, the spatial layout of natural protected areas in Changdao will be optimized with the goals of "rescue protection", "coordinated protection", and "forward-looking protection". The goal of "rescue protection" is an ecological goal, which aims to integrate the overlapping of space and fill the protection gap. The goal of "coordinated protection" is a social goal, which aims to ease the contradiction between the protected areas and their surrounding residential communities, and promote the coexistence of ecology and society. "Forward-looking protection" is an economic goal, that aims to explore the economic benefit provided by these natural protected areas.

4.1 "Rescue protection" optimization

The "rescue protection" optimization aims to solve the problems of overlapping and adjacent connections, and to fill the protection gap. Following the guidance of relevant documents (Ministry of Natural Resources and National Forestry and Grassland Administration, 2020; He et al., 2021), the national nature reserve is treated as the main body, with the other 8 protected areas included, transforming the core protected areas and buffer areas of national nature reserve and provincial seal nature reserve into core protected areas, and the remaining areas are transformed into general control areas. The "protection gap" area included in the protected area mainly considers the spatial coverage of waters where the East Asian finless porpoise appear most, which is located in the east and west sea areas in the middle of the Changdao Island chain (Figure 4) (Wang et al., 2019). This area is little disturbed by human activities, owing to the non-existing aquaculture or submarine pipelines, minor fishing activity that is concentrated mostly in September-April, and less shipping. This area, if protected, will largely improve the habitat for the East Asian finless porpoise (Figure 5).

4.2 "Coordinated protection" optimization

The optimization of "coordinated protection" aims to ease the contradiction between human and nature by adjusting the spatial layout of protected land. The Regulations of the People's Republic of China on Nature Reserves expressly stipulate that "only scientific research and observation activities are allowed in the buffer zone of nature reserves" and "tourism, production and business activities are prohibited in the buffer zone of nature reserves". However, the buffer zone of Changdao National Nature Reserve is filled with many human activities such as aquaculture and shipping (Figure 4). Due to the lack of overall consideration, the national geology park, the Miaodao Islands Provincial Seal Nature Reserve and other protected areas were incorporated into the protected areas at the beginning of their establishment. In particular, the Miaodao Bay area, which is surrounded by the five islands in the south, is intensively disturbed by human activities including raft, bottom seeding, cage farming, shipping, submarine pipeline maintenance, port channel dredging,

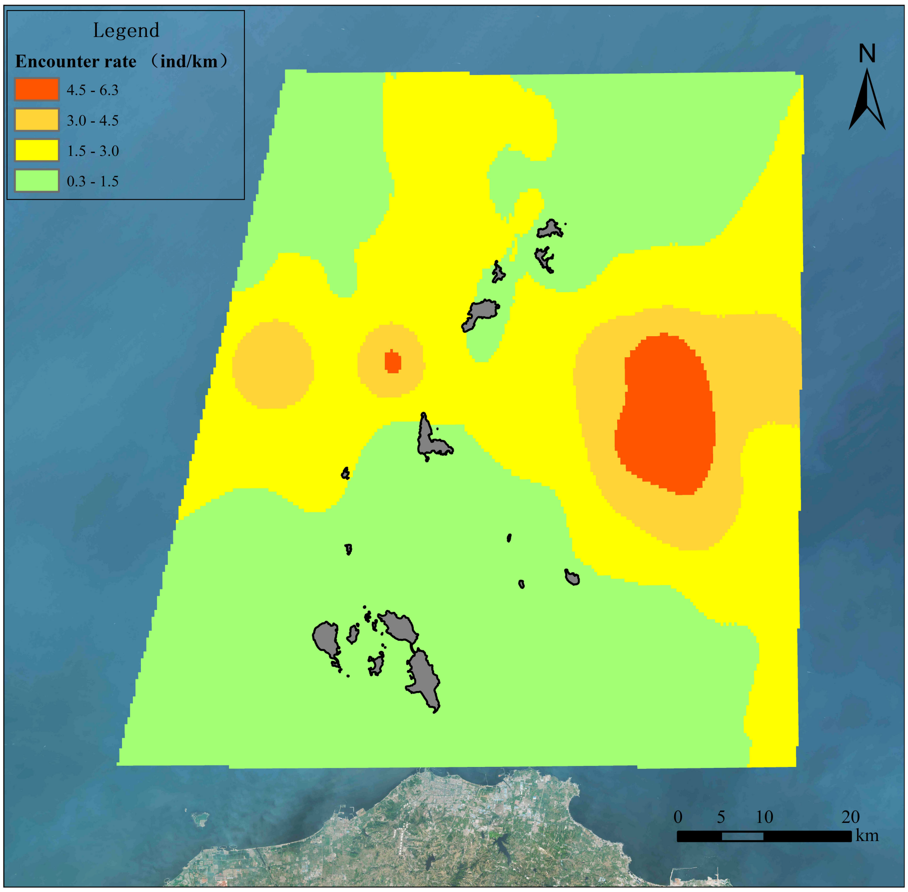

FIGURE 4
Distribution of East Asian Finless Porpoises in Changdao.

urbanization, and etc. These sea waters have low protection value due to the substantial alteration from their original state, and will be a wasted of money if listed as a protected area. Moreover, the sea area is not the habitat for harbor seals, East Asian finless porpoises, and other economic sea production. Excluding it from the protected areas will not affect the inherent ecological connectivity of the sea area. It not cut off the migration route, and destroy the habitats for the key protected species. At the same time, excluding those human-dominated lands from the protected areas, (e.g., agriculture and fishery land, residential land, public facility service land, commercial service land), will not impact the protected targets but will help alleviate the contradiction between protected land and surrounding communities.

After the boundary of the protected area is determined, the internal partition is optimized. The core protected area is a key area to maintain the normal reproduction, and migration of rare animal populations. It is also an important area to realize the complete protection of the island land-intertidal and shallow sea ecosystem, and also an area to adopt the strictest control measures. In order to achieve effective protection of the main conservation objectives, the core areas and buffer areas of existing nature reserves shall be transformed. And original genuine, higher sensitivity to human activities, the forest park of ecological conservation area, the leopard seal, east Asia finless porpoises and active region of rare and endangered Marine life and migration routes, trepang and wrinkles dish bao, light spines ball sea urchins and other marine products native populations the main distribution area of priority to delimit core protection area. All areas outside the core protected areas are included in the general control areas. This area also has high ecosystem authenticity and greater protection value, but it is difficult to implement the strictest control because of the high human disturbance, so it is included in the general control area control.

4.3 “Proactive protection” optimization

The “forward-looking protection” optimization aims to scientifically regulate human activities by adjusting the spatial layout of protected areas and using the management and control measures of protected areas, so that ecological protection and economic development can co-exist. Aquaculture and tourism are the two biggest contributors to the economy of Changdao. If all the aquaculture and tourism areas are excluded from the protected areas, the lack of control measures of the protected areas may lead to a protection crisis due to disorderly breeding and the surge in the number of tourists, and reduce the effectiveness of protection (in the history of Changdao, a large number of scallops died and a decrease in production in successive years due to the disorderly expansion of

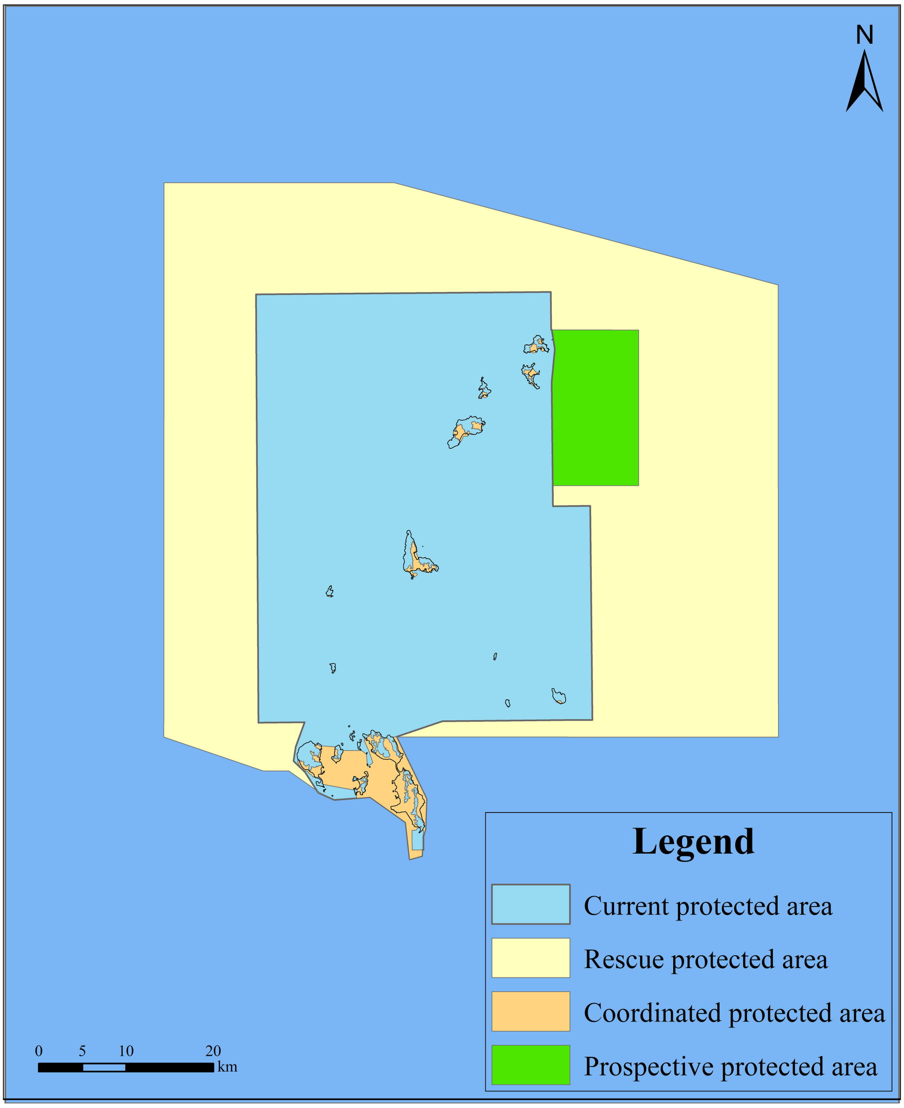

FIGURE 5
Change of Changdao protected area's spatial layout.

aquaculture). Therefore, the concentrated distribution sea area (Figures 5, 6) located in the eastern part of the four islands in the north is included in the general control area of the protected area. The sea area is relatively open, with high flow velocity, and the aquaculture areas are in an open farming mode. This openness will not block the of migratory route for species such as harbor seals and East Asian finless porpoises. Moreover, this will not threaten the ecological environment. At the same time, the control measures of protected areas are used to scientifically control the scale and intensity of aquaculture and tourism based on the ecological environmental carrying capacity, to improve the aquaculture production and tourism services. At the same time, it can also rely on the brand effect and publicity advantages of the integrated national nature reserves or even national parks to provide more high-quality ecological products for the society.

After the above integration and optimization, nine nature protected areas in Changdao were merged into Changdao National Nature Reserve (Figure 7; Table 4), with a total area of 4,269.68 km^2, This area is 2375.03 km^2 larger than the previous one, with the core protected areas and general control areas respectively increased by 1723.1 km^2 and 651.93 km^2. The percentage of core protected areas increased from 17% to 48%, which will be favorable to sustain the authenticity and integrity of the ecosystem. After superposing the development and utilization status of the integrated and optimized protected area spatial layout, the cross-overlap in protected area space and the derived multiple management problems have been eliminated through the integrated optimization, the protection vacancy space of the important habitat of the East Asian finless porpoise has been filled, and the residential area with high human interference and low protection value has been transferred. It will be transferred into the concentrated distribution of marine pastures that will be an important production area of high-quality ecological products to promote development through protection, which can promote the

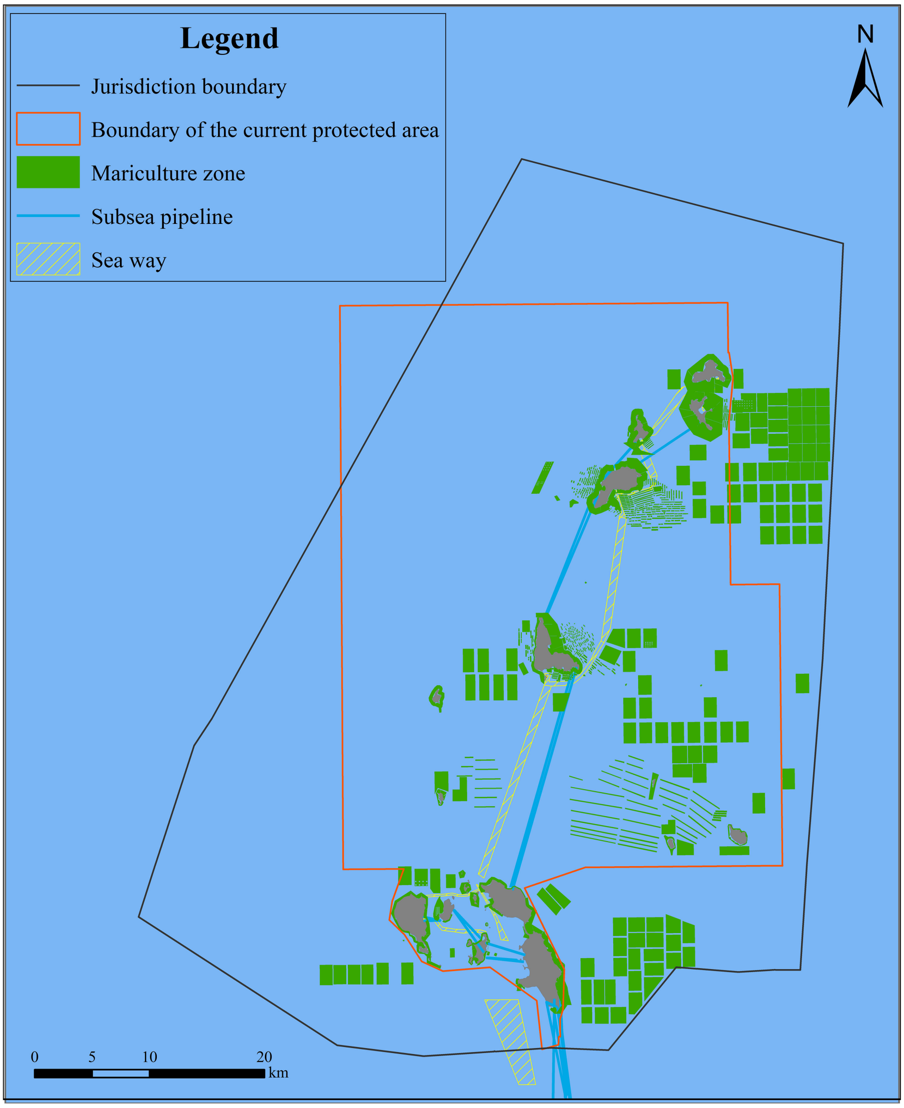

FIGURE 6
Development and utilization status of Changdao.

coordinated development of ecology, society and economy in Changdao.

5 Outlook

The purpose of this study is to explore an integrated optimization method applicable to natural protected areas on islands. This method can jointly protect the key protection objectives, promote the coordinated improvement of the social and economic development of the surrounding communities, and enable the local residents to benefit from ecological protection. Our method used in this study can provide scientific guidance for the integration and optimization of island-type protected areas in China and even in the world. In the future, there is still a high necessity to strengthen the following research directions: (1) At present, China's system of natural protected areas are mainly divided into three types: national parks, nature reserves, and nature parks. Among them, national parks and nature reserves are further divided into core protected areas and general control areas, while the entire area of nature parks is general control area. In order to achieve fine management of natural protected areas, differentiated management strategies, such as time-sharing and zoning, can be explored based on the life history of the main protected objects and their sensitivity to human activities; (2) the habitats of marine organisms are not generally limited to a single natural protected area, especially for those long-distance migratory species. In order to protect the targeted species throughout their lives, further research on ecological corridors and network connectivity of protected areas should be strengthened; (3) In order to enhance the integrated optimization of protected areas on a scientific basis and explore more detailed methods, it is

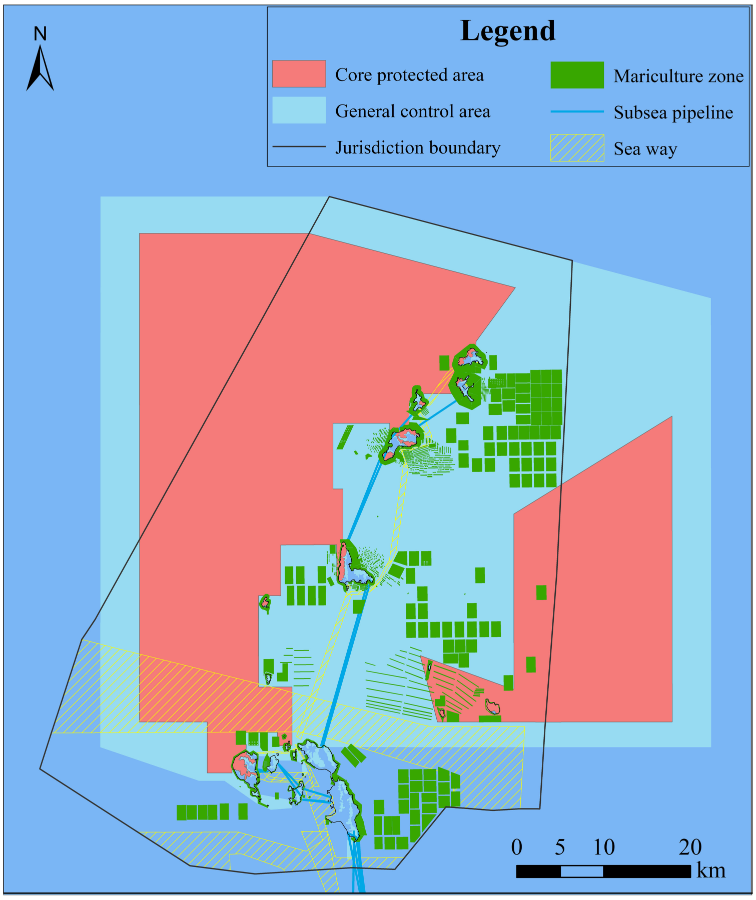

FIGURE 7
The spatial layout of Changdao protected area after integration and optimization.

TABLE 4 The area changes of Changdao protected areas before and after integration and optimization (km^2).

	Total	Core protected area		General control area	
		Area	proportion	Area	proportion
before	1894.65	328.09	17%	1566.56	83%
after	4269.68	2051.19	48%	2218.49	52%

necessary to improve the evaluation framework of ecosystem integrity and authenticity of protected areas; (4) In order to fully demonstrate and continuously track all aspects of the impact brought by the integration and optimization of protected areas, it is necessary to carry out studies on socio-economic impact assessment and performance evaluation of protected areas.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

SH: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft. TX: Data curation. ML: Methodology, Resources, Validation, Writing – review & editing. WL: Conceptualization. JZ: Data curation. YL: Investigation, Data curation. SC: Project administration, Investigation.

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Conflict of interest

Publisher's note

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An integrated methodological framework for the durable conservation of freshwater ecosystems: a case study in Colombia's Caquetá River basin

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Introduction: Although freshwater ecosystems encompass 12% of all known species, their study has achieved less progress in systematic conservation planning exercises compared with terrestrial and marine ecosystems. Moreover, little attention has been given to ecosystem services and cultural and spiritual values, which are pivotal in the long-term preservation of freshwater ecosystems. Conservation, restoration, and sustainable management actions within freshwater systems are currently addressed individually, underscoring the necessity of comprehensive methodological frameworks that holistically address the questions of where and how to conserve while integrating ecosystem services and cultural factors as conservation values.

Methods: We propose a new methodological framework for the conservation of freshwater ecosystems that incorporates these elements and fulfills six prioritization criteria: 1) representativeness, 2) integrity, 3) importance, 4) rarity, 5) complementarity, and 6) connectivity. To illustrate the application of this approach, we conducted a regional study in the Caquetá River basin in Colombia.

Results: By applying our methodological framework, we demonstrated that the Caquetá River basin hosts 518 distinct freshwater groups with unique characteristics that contribute to the maintenance of ecosystems and the preservation of their inherent values. Additionally, our analysis revealed that protection is the most effective conservation strategy for 77.4% of the Caquetá River basin, whereas restoration and sustainable management are suitable for 4.7% and 17.9% of the basin, respectively. The prioritized portfolio for the Caquetá River basin encompasses 80.1% of all freshwater groups, effectively meeting The Nature Conservancy's proposed conservation objectives.

Conclusion: This novel methodological framework provides a pragmatic approach to systematic conservation planning and answers the questions of both where and how to conserve.

KEYWORDS

Caquetá River, durable freshwater protection, integrity, representativeness, importance, prioritization, systematic conservation planning, Amazon

1 Introduction

Systematic conservation planning (SCP) is a process aimed at identifying and preserving areas with high conservation value (Kukkala and Moilanen, 2013; Beyer et al., 2016). The most significant progress in SCP has been made in terrestrial and marine ecosystems (Darwall et al., 2011); SCP in freshwater ecosystems has lagged (Nogueira et al., 2023) despite their high species richness (~12% of all known species) in a very small fraction of Earth's surface area (~2%) (Garcia-Moreno et al., 2014; Román-Palacios et al., 2022). The amount of scientific research focused on aquatic systems, including freshwater ecosystems, increased by 60% between 2010 and 2017 (Di Marco et al., 2017), reflecting the need for research on SCP to strengthen decision-making and help counteract the degradation these ecosystems are exposed to (Harrison et al., 2018; Grill et al., 2019; Desforges et al., 2022).

SCP efforts have prioritized defining protected areas to preserve biodiversity (Hermoso et al., 2011; 2018; Tognelli et al., 2019; Dorji et al., 2020; Linke and Hermoso, 2022; Nogueira et al., 2023), overlooking other equally important aspects, such as ecosystem services and cultural and spiritual values, which support societal wellbeing. Recently, Higgins et al. (2021) proposed a conceptual methodological framework to guide the development of more effective conservation strategies for freshwater ecosystems. According to these authors, durable conservation of freshwater ecosystems must incorporate ecosystem services and cultural and spiritual values as conservation values. Doing so will enable the integration of community-driven conservation strategies through the management of common resources, thereby enhancing conservation outcomes (Campos-Silva and Peres, 2016; Garnett et al., 2018; Fa et al., 2020).

Higgins et al. (2021) also argued that the essential characteristics of ecosystems, or key ecological attributes (KEAs), must be identified to maintain the persistence of conservation values (e.g., hydrological regime, connectivity, water quality, physical structure). According to the authors, identifying KEAs also allows for the precise identification of threats to freshwater ecosystems and can guide the selection of appropriate conservation actions and mechanisms to reduce or mitigate these threats in the long term. SCP has attempted to answer fundamental conservation questions, including what should be prioritized for conservation and where it is most cost-effective to do so (Dorji et al., 2020; Pienkowski et al., 2021). However, the question of how to conserve has, so far, been addressed separately (Howard et al., 2018; Mu et al., 2022). Though numerous researchers have focused on defining areas for protection (Tognelli et al., 2019; Szabolcs et al., 2022; Valencia-Rodríguez et al., 2022; Nogueira et al., 2023), SCP frameworks must include other strategies, such as restoration and sustainable management. The freshwater biodiversity emergency recovery plan (Tickner et al., 2020) recognizes the importance of restoration and sustainable management as necessary actions for the conservation of biodiversity, cultural values, and ecosystem services (Janishevski et al., 2015; Arthington, 2021; Mu et al., 2022). Therefore, as stated by Higgins et al. (2021), SCP exercises must integrate different conservation actions with protection to expand the options for selecting legal mechanisms for conservation and the criteria for designing specific conservation activities.

Riato et al. (2020) proposed a multi-scale methodological approach that links KEAs and their threats through an integrity index, which is used to prioritize protection, restoration, and sustainable management actions in rivers and streams, particularly for benthic communities. Other authors have also made valuable contributions; for example, Mu et al. (2022) proposed a methodological framework based on SCP theories to identify optimal sites for cost-effective protection and restoration that consider ecosystem services, such as water yield and carbon storage, as conservation values. Furthermore, Cattarino et al. (2015) proposed a novel algorithm for prioritizing multiple conservation actions within the same site, assuming that threats to freshwater ecosystems can be mitigated by selecting a specific conservation action. This algorithm also considers the inherent connectivity of freshwater ecosystems, building upon the advances by Hermoso et al. (2011). The proposal presented by Riato et al. (2020) stands out among these methodologies by including the concept of basin integrity. This proposal is particularly interesting given its multi-scale approach to the identification of conservation actions, as it inherently evaluates the basin's capacity (based on its integrity) to support a particular action. Furthermore, the scheme proposed by Riato et al. (2020) is highly adaptable because it does not depend on a specific tool or dataset, giving it great practicality and operability (Riato et al., 2020; 2023).

The efforts mentioned above that incorporate one or several of the criteria described by Higgins et al. (2021) highlight the need for new methodological frameworks that comprehensively address the questions of where and how to conserve. However, although Higgins et al. (2021) described the criteria that should be considered to achieve durable protection of freshwater ecosystems, they did not specify how these criteria should be applied within the context of an SCP process to provide an integrated response to these questions. Therefore, we aimed to develop a new methodological framework for freshwater ecosystem conservation that consolidates and articulates the concepts proposed by Higgins et al. (2021) in an SCP environment. Furthermore, we include the methodological scheme proposed by Riato et al. (2020) to simultaneously address the questions of where and how to conserve.

To achieve our goal, we integrated various models and analytical tools to employ a set of indexes with six prioritization criteria: i) representativeness, ii) integrity, iii) importance, iv) rarity, v) complementarity, and vi) connectivity. Given the Amazon is one of the few megadiverse regions in the world where freshwater biodiversity remains relatively healthy, we used the dam-free Caquetá River basin in the Amazon region of Colombia as a case study (Albert et al., 2011; Anderson et al., 2018; He et al., 2018; Caldas et al., 2023). The Amazon is also home to several Indigenous and local communities that have deep social, cultural, and economic connections with the intricate network of freshwater ecosystems (Campos-Silva and Peres, 2016; Garnett et al., 2018; Fa et al., 2020).

2 Methodological framework

The methodological framework we propose for the SCP of freshwater ecosystems incorporates six criteria commonly used for prioritization (Kukkala and Moilanen, 2013; Linke and Hermoso, 2022; Valencia-Rodríguez et al., 2022): i)

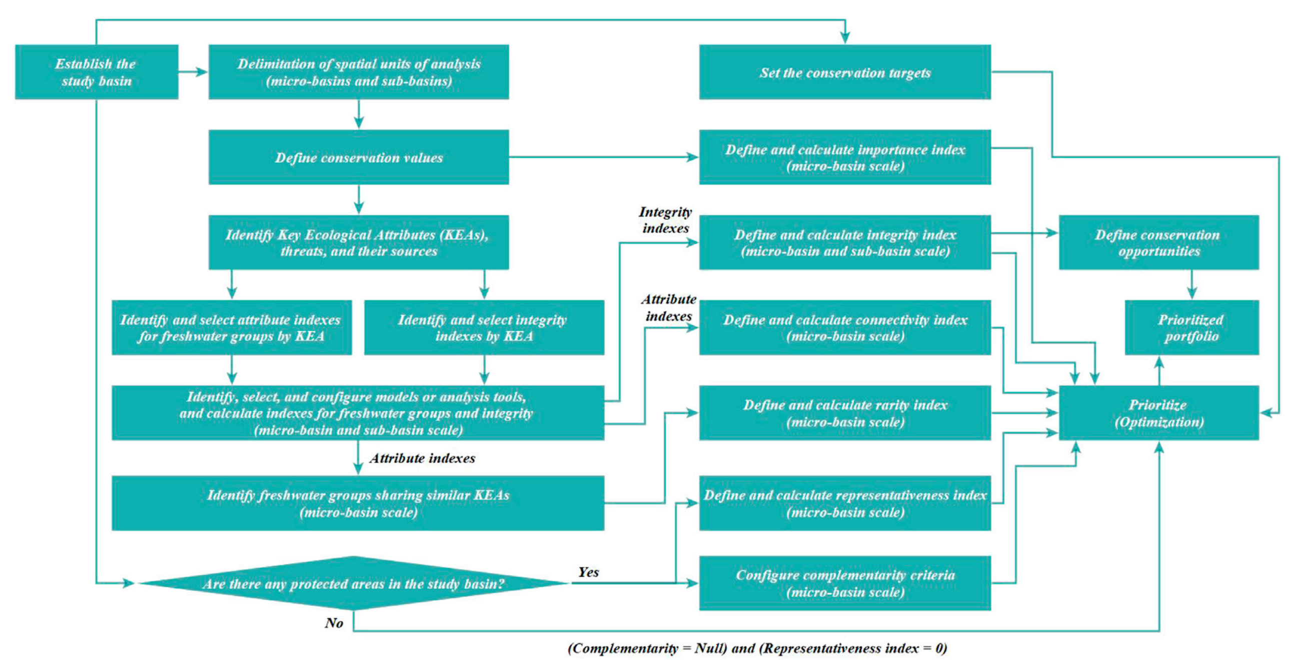

FIGURE 1
Proposed methodological framework for integrated planning of freshwater ecosystems.

representativeness, which prioritizes ecosystems not already under a conservation figure (e.g., protected areas); ii) integrity, which favors ecosystems with less pressure on their KEAs; iii) importance, which prioritizes ecosystems with greater conservation values; iv) rarity, which promotes the selection of unique ecosystems; v) complementarity, which accounts for existing conservation zones; and vi) connectivity, which promotes the connection between ecosystems. Figure 1 schematically depicts the proposed methodological framework, which uses indexes to quantify each of the established prioritization criteria.

We selected the indexes following the criteria described by Higgins et al. (2021). All indexes were estimated at the micro-basin scale, as this is the planning unit considered for the portfolio. Specifically, for the criterion of integrity, our methodology involves calculating this index at two scales: i) micro-basin and ii) sub-basin. These two scales are linked through the framework proposed by Riato et al. (2020), with which we selected the best conservation opportunities (actions).

Finally, the indexes are integrated into a mathematical optimization scheme to select priority areas. The resulting prioritized conservation portfolio combines the priority areas with conservation opportunities. Each of the steps in our methodological proposal is detailed below.

2.1 Establishing the study basin

The first phase of our methodology involves defining the study area, gathering all the secondary information, and defining the field campaigns necessary for the study. At this stage, it is also important to identify the existence of previously established protected areas in the study area as the criteria for representativeness and complementarity depend on this information.

2.2 Setting the conservation targets

Defining conservation objectives serves several purposes. For example, it facilitates the selection of the minimum area necessary to represent and ensure the persistence of conservation values (Linke et al., 2011). These objectives may be established considering the economic constraints related to investment in actions, or they may simply be a product of the specific goals of an organization or group of organizations (Téllez et al., 2011). In this methodological framework, the conservation objectives are set as input criteria for prioritization (see Step 2.17), allowing conservationists to address specific questions or interests.

2.3 Delimitation of spatial units of analysis

Following the proposal by Riato et al. (2020) to select conservation actions (see Step 2.16) using the integrity criterion, our framework uses micro-basins and sub-basins as the scales of analysis. We based our scales on basins as they are appropriate units for the SCP of freshwater ecosystems (Tognelli et al., 2019; Dorji et al., 2020; Linke and Hermoso, 2022; Nogueira et al., 2023). This stage of our proposal consists of automatically delimiting these units using a digital terrain elevation model (DEM), which allows us to obtain the units of analysis and the river segments between two consecutive nodes or within the units. This approach produces a graph representation of the study area that defines the connectivity between the units, which facilitates efficient cumulative calculations (important aspects for Steps 2.8, 2.11, and 2.17).

2.4 Defining conservation values

According to Higgins et al. (2021), conservation values refer to various aspects, such as species, ecosystem services (cultural, provisioning, supporting, and regulating), as well as cultural and spiritual values that are important to a particular community. In our methodology, it is possible to consider one or several of these elements; the number of values to consider will depend on their level of relevance in the selected study area. At the end of the process, conservation values are condensed into a numerical index that we have defined as an index of importance (in Step 2.13).

2.5 Identification of KEAs, threats, and their sources

KEAs are essential characteristics for the maintenance of freshwater ecosystems and, therefore, for the conservation values (Higgins et al., 2021). Existing research has identified the hydrological regime, sediment transport, water quality, physical structure, and connectivity as the main determinants of the physical habitat and biotic communities of freshwater ecosystems (Poff et al., 1997; Castello et al., 2013; Zeiringer et al., 2018; Higgins et al., 2021). In turn, these characteristics shape the social dynamics of communities that depend on these ecosystems for their livelihoods. Therefore, this methodology prioritizes these KEAs for analysis.

Threats, on the other hand, are factors that generate stress on KEAs—e.g., climate change, deforestation, pollution, and dam construction (Poff et al., 1997; Castello et al., 2013; Dudgeon, 2014; Alho et al., 2015; Arthington et al., 2016; Zeiringer et al., 2018)—resulting in ecosystem degradation (Higgins et al., 2021). Therefore, the KEAs, the threats to the KEAs, and the sources of the threats must be selected depending on the study basin. This step is crucial because these decisions will determine the indexes, models, or analysis tools to be used in the study.

2.6 Identification and selection of attribute indexes for freshwater groups by KEA

A freshwater group is a set of planning units, or micro-basins, that possess similar KEAs. In this sense, freshwater groups can be understood as collections of habitats within a basin. Our proposed framework employs simple characteristics and indexes for each KEA, allowing for precise differentiation of areas with unique KEAs without requiring extensive amounts of information for their configuration. The freshwater groups are of great importance in our proposal because we understand them as the freshwater habitats present in the basin. Additionally, the rarity and representativeness criteria are derived from these groups.

2.7 Identification and selection of integrity indexes by KEA

Our methodology considers integrity as the capacity of a basin to support and maintain the broad range of ecological processes and functions essential for both biodiversity sustainability and the resources and services that the basin provides to society (Flotemersch et al., 2016). Based on this definition, our framework uses a set of indexes to assess how the identified threats (in Step 0) may impact the KEAs in the study basin, in turn affecting ecosystem integrity.

2.8 Identification, selection, and configuration of models or analysis tools and calculation of indexes for freshwater groups and integrity

The selection of models and analysis tools is based on the indexes defined for the freshwater and integrity groups. The selected tools must be sensitive to the threats identified in each KEA. Our framework is flexible and allows for the adoption of different approaches and strategies, such as a conceptual approach (Thornbrugh et al., 2018), machine learning (Giri et al., 2019), empirical models, or a combination of these (Einheuser et al., 2013). Moreover, it is possible to select individual tools for each KEA or to use the same tool to model multiple KEAs.

Once the models and analysis tools have been chosen, this stage also includes collecting and processing the information needed to build the models, configuring and running the selected models, and calculating the indexes corresponding to the river and integrity groups.

2.9 Identification of freshwater groups sharing similar KEAs

In this step, the defined attribute indexes are used to group the planning units to identify freshwater clusters. Different clustering approaches can be used to achieve this, including hierarchical, partitional, grid, density-based, or model-based methods (Saxena et al., 2017). The choice of method will depend on the characteristics (qualitative or quantitative) of the attribute indexes selected in Step 2.6. Our goal in identifying freshwater group clusters is to generate connected corridors of high–conservation value micro-basins that host the greatest possible diversity of freshwater groups (representativeness criterion) and include the rarest freshwater groups (rarity criterion).

2.10 Defining and calculating the rarity index

In our methodology, rarity is a measure of the uniqueness or scarcity of a given freshwater group within the study basin, or the proportion or area occupied by that group compared with the rest of the groups present in the basin. Rarity is a criterion in the prioritization process, as described in Step 2.17. Thus, in this phase, we construct an index that reflects the rarity of each freshwater group in the basin using a formula that considers the proportion or relative area occupied by the group in relation to all the groups present. This process produces a numerical index that captures the rarity of each group, enabling the subsequent comparison and prioritization of the groups in the basin.

2.11 Defining and calculating the connectivity index

Because impacts on aquatic ecosystems are cumulative, we seek to foster connectivity in the prioritized micro-basins due to the importance of connectivity for freshwater ecosystems (Saura et al., 2017; Herrera-Pérez et al., 2019). Therefore, in this step, we construct an index that reflects the degree of connection between two micro-basins to prioritize corridors of connected micro-basins linking headwater rivers (see Step 2.17). This index is based on the proximity between micro-basins, measured from their centroids or across their river segments. Key references for the construction of this index were Hermoso et al. (2011, 2018), Cattarino et al. (2015), Wohl (2017), and Dorji et al. (2020).

2.12 Defining and calculating the integrity index

In our proposal, integrity plays a fundamental role in both prioritization (see Step 2.17) and the definition of conservation opportunities (see Step 2.16). Both steps require a single index ranging from 0 to 1, where 0 represents low integrity and 1 represents high integrity. Therefore, this step involves constructing an integrity index that groups the indexes defined in Step 2.7 and calculated in Step 2.8. This can be accomplished using aggregation methods, such as geometric or arithmetic aggregation (Juwana et al., 2012), or multiplicative approaches, such as those used by Thornbrugh et al. (2018).

2.13 Defining and calculating the importance index

The concept of importance in our methodology is closely related to the quantity of conservation values present in a micro-basin. As described in the prioritization section (see Step 2.17), our methodology seeks to maximize importance while achieving the conservation target. In this phase, we construct a numerical index ranging from 0 to 1, where 0 denotes the total absence of conservation values and 1 represents a high concentration of conservation values. One possible approach is to assign a relative weight (between 0 and 1) to each conservation value identified in Step 2.4 and calculate a weighted average of these values. This would provide an index that reflects the overall importance of the conservation values present in the micro-basin.

2.14 Defining and calculating the representativeness index

Our methodological framework defines representativeness as a measure of the presence of freshwater groups in the network of existing protected areas in the study area. The representativeness index can be constructed by considering the area of the freshwater group and the area covered within the protected areas (Duarte et al., 2016). If there are no protected areas in the study area, this index will have a value of 0 for all the micro-basins.

2.15 Configuring complementarity criteria

Complementarity in our methodology refers to the inclusion in the priority portfolio of those freshwater groups that are not represented in protected areas. This concept is closely related to that of representativeness. Therefore, our methodology incorporates this criterion as a constraint in the prioritization process (see Step 2.17) to ensure that the priority portfolio includes existing protected areas in the study area. If there are no protected areas in the study area, this criterion is not considered in the prioritization.

2.16 Defining conservation opportunities

We followed the proposal of Riato et al. (2020) to define conservation opportunities, including protection, restoration, and sustainable management, using the integrity index estimated at the micro-basin and sub-basin levels. The process begins by contrasting the indexes on a 2D scatterplot (both indexes should be scaled between 0 and 1, where 0 represents low integrity and 1 represents high integrity). Then, four quadrants are defined, centered on the 0.5 value of each index. If both the micro-basin and sub-basin indexes show values greater than 0.5, the ecosystem is in good condition; thus, it would be best to consider a protection action because doing so would require minimal intervention. If, instead, the index at the sub-basin scale is greater than 0.5 but the index at the micro-basin scale is less than 0.5, it would be more appropriate to consider restoration as the best conservation opportunity because a healthy sub-basin can support this action. However, if both indexes have values below 0.5, sustainable management would be the best option. In this case, protection and restoration would require considerable effort and resources because they would not be supported by good conditions at either scale.

2.17 Prioritization and optimization

SCP aims to maximize the representation of conservation objects. In our case, it involves identifying the network of micro-basins that maximizes conservation values (importance) while i) promoting the highest representativeness of freshwater groups, ii) connecting the largest number of rare freshwater groups, iii) including micro-basins with high integrity, and iv) generating corridors of connected micro-basins. To achieve this, we relied on the proposal by Hermoso et al. (2011) to formulate the following optimization objective function (Of):

$$Of = \left(\sum_{\substack{Micro\text{-}basin}} I_{CV} \right) + \left(\sum_{\substack{Integrity \\ penalty}} -I \right) + \left(\sum_{\substack{Rarity \\ penalty}} I_R \right) + \left(\sum_{\substack{Representativity \\ penalty}} I_{Rep} \right) + \left(\sum_{\substack{Connectivity \\ penalty}} -CI \right)$$

We propose using the integrity, rarity, representativeness, and connectivity indexes as penalties (with equal weights) along with a constraint that ensures the selection of micro-basins located within existing conservation areas. Thus, micro-basins with lower integrity, higher abundance of a freshwater group, and

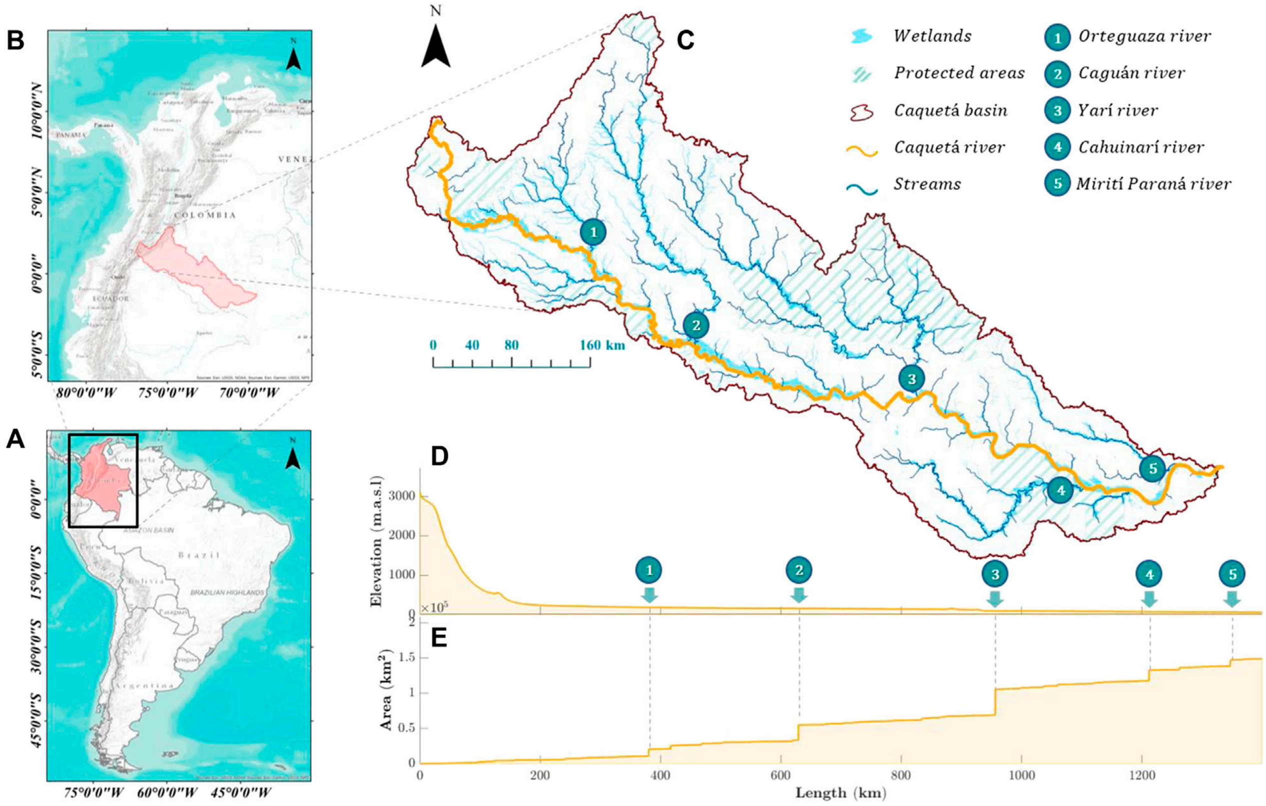

FIGURE 2
Caquetá River basin. **(A)** Location in South America. **(B)** Location in Colombia. **(C)** Hydrographic map of the Caquetá River basin and main rivers. **(D)** Elevation profile of the Caquetá River. **(E)** Profile of accumulated area (tributaries) on the Caquetá River.

representation in existing conservation areas will be penalized more significantly.

2.18 Prioritized portfolio

The conservation portfolio is composed of the priority areas resulting from the optimization process and the conservation opportunities identified from the 2D scatterplot proposed by Riato et al. (2020), which must be addressed to achieve the established conservation objectives.

3 Materials and methods

3.1 Study area

For the application of our methodological framework, we considered the Caquetá River basin, which covers an area of 148,763 km^2 and represents 31% of the Colombian Amazon biome (Figures 2A–C). This region has an altitudinal gradient of 4,200–60 masl (Figure 2D), generating a spatially variable annual precipitation range of 790–4,924 mm. The climate is characterized by two rainy seasons per year in the mountain zone (March–May and October–December) and one season in the central and foothill zones (April–June). These climatic conditions foster a wide range of cold to warm tropical environments.

The Caquetá River is 1,400 km in length and collects the waters from other important rivers, such as Orteguaza (696 m^3/s), Caguán (1,142 m^3/s), Yarí (2,138 m^3/s), Cahunarí (986 m^3/s), and Mirití Paraná (654 m^3/s), reaching an average annual flow of 10,100 m^3/s. Approximately 13% of its drainage area is wetlands, of which 18% have been intervened on or transformed by anthropic actions (Ministerio de Ambiente Desarrollo Sostenible, 2021). Currently, 21% of the basin is protected by 10 natural parks (Figure 2C) (Parques Nacionales Naturales de Colombia, 2020).

The characteristics of the Caquetá River basin support biodiversity in its freshwater ecosystems. More than 400 fish species have been recorded in the different tributaries (Celis-Granada et al., 2022). The Caquetá River is also an important migratory corridor for 23 species, including turtles (e.g., *Podocnemis expansa*), fish (e.g., *Brachyplatystoma rousseauxii*), and dolphins (e.g., *Sotalia fluviatilis*) (He et al., 2018; 2021; Caldas et al., 2023). Cultural richness is also a distinctive feature of this area, which is home to Indigenous, peasant, and Raizales communities (Agencia Nacional de Tierras, 2023). Indigenous communities have a greater presence in the territory, with 96 legally constituted Indigenous reserves occupying 43% of the total area and bringing together peoples such as the Murui-Muinane, Yucuna, Andoque, Inga, and Coreguaje, among others

(Agencia Nacional de Tierras, 2023). There is also recorded evidence of uncontacted isolated communities in this region (Seifart and Echeverri, 2014; Walker et al., 2016; Walker and Hamilton, 2019).

3.2 Conservation targets

Recognizing the global importance of the Amazon River basin for the conservation of freshwater biodiversity and the communities that depend on it, The Nature Conservancy has prioritized this area in its conservation vision for 2030 (The Nature Conservancy, 2022). As part of this commitment, they have embarked on a conservation planning process to establish a roadmap for their future work, thereby helping to preserve the biodiversity and the values it supports. To achieve this, The Nature Conservancy developed a conservation plan for the Amazon River basin with the following objectives, which we have considered for the Caquetá River basin.

- Conserve 80% of the main rivers (large and very large; flow >100 m^3/s), ensuring connected corridors that remain functional/healthy.
- Conserve 30% of the headwater rivers (small and medium-sized; flow ≤100 m^3/s), ensuring connected corridors to the main channels that remain functional/healthy.

The materialization of these objectives by The Nature Conservancy would contribute to Target 3 of the United Nations Convention on Biological Diversity: to protect and effectively manage 30% of the world’s terrestrial, inland waters, and coastal and marine areas by 2030 (ONU, 2022).

3.3 Spatial units of analysis

To delimit the micro- and sub-basins of the Caquetá River basin, we used the Shuttle Radar Topography Mission DEM with a 90-m resolution (Jarvis et al., 2008). We processed the DEM using ArcGIS 10.7 and ArcHydro Tools. To delimit micro-basins, we used an area accumulation threshold of 2.8 km^2. However, in areas where the river profile showed a steeper slope than the adjacent segments, known as knickpoints, we performed an additional segmentation. For this subdivision, we considered the geomorphological conditions of the areas and the habitats they provide (Ross et al., 2001) and used the algorithm proposed by Hayakawa and Oguchi (2006) to detect the knickpoints. We defined the sub-basins according to the delimitations established by the environmental authority, Corporación para el Desarrollo Sostenible del Sur de la Amazonia (Corpoamazonía), so the proposed conservation portfolio can be effectively integrated with territorial planning instruments.

3.4 Conservation values

We considered the following conservation values for the Caquetá River basin:

Species: i) We obtained information on 55 species of fish, 47 species of amphibians, and 102 species of aquatic birds from the collaborative BioModelos system of the Alexander Von Humboldt Institute (Velásquez-Tibatá et al., 2019). ii) We considered the distribution of four species (*Pteronura brasiliensis, S. fluviatilis, Tapirus terrestres, Tapirus pinchaque*) in danger of extinction as reported by the IUCN (2022). iii) Data on megafauna species and their migratory corridors were taken from Caldas et al. (2023) and He et al. (2018), respectively.

Ecosystem services: Recreation and tourism were integrated based on the distribution of recreation person-days, which we generated using the InVEST Visitation: Recreation and Tourism model (Natural Capital Project, 2022).

Cultural areas: Ninety-six Indigenous reserves were included from two areas of the Raizales community and one peasant reserve, using the information reported by Agencia Nacional de Tierras (2023).

Spiritual areas: Sacred and spiritual sites for Indigenous communities were defined according to Organización Nacional de los Pueblos Indígenas de la Amazonia Colombiana (2017), considering the importance they represent for the cosmovision of Indigenous peoples (The Nature Conservancy and The Amazon Conservation Team, 2019).

3.5 KEAs, threats, and their sources

In Amazonian freshwater ecosystems, including the Caquetá River basin, deforestation is primarily driven by agricultural and livestock expansion. These activities are also sources of phosphorus and nitrogen pollution resulting from the fertilization of pastures and crops. Other sources of pollution include oil and gas concessions and legal and illegal mining activities, the latter of which is primarily associated with mercury contamination from gold extraction (Castello et al., 2013). According to Diaz et al. (2020), Colombia is among the countries that use the greatest amount of mercury to produce one ton of gold (4.19 Hg/ton). Moreover, climate change has reduced precipitation and increased temperatures in the Amazon (Killeen and Solórzano, 2008). The Caquetá basin does not currently have hydropower development modifying water and sediment flows or disrupting the river network. Table 1 summarizes the main threats and the sources that we considered in our analysis, according to the selected KEAs.

3.6 Freshwater group indexes

Here, we describe the indexes selected for each KEA in the case study.

Hydrological regime: We considered the components of the hydrological regime (magnitude, frequency, duration, timing, and rate of change) using the following hydrological signatures of the Caquetá River (McMillan, 2020; 2021): i) mean annual flow (magnitude), ii) high flow duration (duration), iii) frequency of peak flow (frequency), iv) slope of the flow duration curve (rate of change), and v) mean half flow date (timing) (Table 1).

Sediment transport: We estimated the sediment transport capacity under bankfull conditions as an index for this KEA (Table 1).

TABLE 1 Key ecological attributes (KEAs), main threats, their sources and attribute and integrity indexes selected for the Caquetá River basin.

KEAs	Threats	Source	Attribute indexes	Integrity indexes
Hydrological regime	Climate change	Precipitation and temperature variations	Magnitude: mean annual flow	Index of percentage variation in the duration curve percentiles of streamflow (I_{HR})
			Duration: high flow duration	
			Frequency: seasonality of high flow	
			Rate of change: slope of flow duration curve	
			Timing: high flow date	
Sediment flow	Climate change	Agriculture	Average sediment transport capacity in bankfull condition	Index of percentage variation in the duration curve percentiles of sediment flow (I_{ST})
	Deforestation	Livestock		
		Precipitation and temperature variations		
Water quality	Pollution	Agriculture	Backwater river Whitewater river Clearwater river	Water quality index (I_{WQ})
		Livestock		
		Legal and illegal mining		
		Oil and gas concessions		
Physical structure	Deforestation	Agriculture livestock	Confined	Stressor mapping index (I_{PS})
		Infrastructure	Unconfined	
		Fires	Capacity-limited	
			Supply-limited	
Connectivity	Hydropower plants	Without current sources	Dendritic connectivity index	Longitudinal connectivity index (I_C)

Water quality: For Amazonian environments, three types of water have been defined in terms of chemical composition (Ríos-Villamizar et al., 2013): i) blackwater rivers, ii) clearwater rivers, and iii) whitewater rivers (see Table 1).

Physical structure: Considering the importance of biotic productivity (Venarsky et al., 2018) and available habitats in freshwater ecosystems (Flores et al., 2006; Buffington and Montgomery, 2022), we selected the following indexes to assess the study area's physical structure: i) the morphological configuration of the river, which can be confined or unconfined, and ii) the specific stream power, which can be capacity- or supply-limited (Table 1).

Connectivity: Connectivity is an essential attribute of freshwater ecosystems (Saura et al., 2017; Herrera-Pérez et al., 2019), particularly for fish that perform migratory movements in the Caquetá River basin, such as the *B. rousseauxii* catfish (Córdoba et al., 2013). For this KEA, we have selected the dendritic connectivity index, as proposed by Cote et al. (2009) (Table 1).

Step 3.9. details how we used these attribute indexes to identify freshwater groups.

3.7 Integrity indexes

Hydrological regime and sediment transport: Based on the hydrological alterations concept by Poff et al. (2010), we created an index that allows us to evaluate the impact of the climate change threat on the hydrological regime and sediment transport. The mass flow index (I_{HR} or I_{ST}, according to the considered variable) assesses the average percentage variation of the p percentiles of the duration curve (5, 10, 15, . . ., 95) of streamflow (Q) or sediment transport (Q_S) between a historical condition (h) and a climate change condition (cc):

$$I_{HR} = \frac{1}{N}\sum_{p=1}^{Np}\left|\frac{Q_{p,cc} - Q_{p,h}}{Q_{p,h}}\right|$$

$$I_{ST} = \frac{1}{N}\sum_{p=1}^{Np}\left|\frac{Qs_{p,cc} - Qs_{p,h}}{Qs_{p,h}}\right|$$

where Np is the number of percentiles of the streamflow or sediment flow duration curve.

Water quality: We considered the following water quality index (I_{WQ}) (Orjuela and Lopez, 2011; Akhtar et al., 2021) as representative of the river's chemical composition in our study area:

$$I_{WQ} = \sum_{d=1}^{Nd} W_d \times S_{WQd}$$

$$\left(\sum_{d=1}^{Nd} W_d\right) = 1$$

where S_{WQd} is the value of the sub-index for water quality determinant d, which has a value between 0 and 1; Nd is the number of water quality determinants considered; and W_d is the

TABLE 2 Sub-indexes considered for each of the water quality determinants considered in the water quality index and stress factors considered to affect physical structure.

Sub-indexes for each of the water quality determinants		
Water quality determinants	Sub-index functions	Source
Dissolved oxygen	$S_{WQDO} = (1 - (0.01 * \frac{DO}{O_s}))$	Orjuela and Lopez (2011)
Suspended solids	$S_{WQSS} = 1 - (-0.02 + (0.003 * SS))$	Orjuela and Lopez (2011)
Total nitrogen (NO + NH_4 + NO_3)	$S_{WQTN} = 1 - (0.5 \log_{10} TN)$	Armida (2007)
Total phosphorus (Po + Pi)	$S_{WQTP} = 1 - (0.6 + 0.4 \log_{10} TP)$	Armida (2007)
Pathogenic organisms	$S_{WQX} = 1 - (-1.44 + 0.56 \log_{10} X)$	Armida (2007)
Organic matter	$S_{WQOM} = 1 - (-0.05 + 0.7 \log_{10} OM)$	Ramirez et al. (1997)
Total mercury	$S_{WQTHg} = if \begin{cases} (THg > 0.001 \text{ mg/l}) = 0 \\ (THg \leq 0.001 \text{ mg/l}) = 1 \end{cases}$	Ministerio de Salud y Protección Social, and Ministerio de Ambiente y Desarrollo Sostenible (2007)
Stress factors considered to affect physical structure		
Stressor (S_z)	Unit	Source
Presence of roads	m	Instituto Geográfico Agustín Codazzi (2022)
Presence of urban area	m^2	Departamento Administrativo Nacional de Estadística (2018)
Presence of oil wells	number	Agencia Nacional de Tierras (2023)
Presence of mining titles	m^2	Unidad de Planeación Minero Energética (2022b)
Density of burning areas	m^2/m^2	Instituto Amazónico de Investigaciones Científicas (2022a)
Density of deforested area	m^2/m^2	Instituto Amazónico de Investigaciones Científicas (2020)
Density of transformed wetlands	m^2/m^2	Burbano-Girón et al. (2020)

weighting factor. We used equal weights for each determinant with a value of $1/Nd$. The subscripts for each considered water quality determinant are presented in Table 2.

In Table 2, SS is the suspended solids concentration (mg/L); X is the concentration of pathogenic organisms (NMP/100 mL); TN is the total nitrogen concentration (mg/L), which includes organic nitrogen, ammoniacal nitrogen, and nitrates; TP is the total phosphorus concentration (mg/L), which includes organic and inorganic phosphorus; OM is the organic matter concentration (mg/L); DO is the dissolved oxygen concentration (mg/L); O_s is the saturation oxygen concentration (mg/L); and THg is the total mercury concentration (mg/L), which includes elemental, divalent, and methyl mercury. For total mercury, we considered a binary sub-index with two categories (good = 1 and bad = 0), according to the permissible limit (0.001 mg Hg/L) defined by Ministerio de Salud y Protección Social and Ministerio de Ambiente Desarrollo Sostenible (2007) for Colombia.

Physical structure: We adapted a stressor mapping index (I_{PS}) from Flotemersch et al. (2016) by applying a geometric aggregation method (Juwana et al., 2012):

$$I_{PS} = \prod_{z=1}^{Nz} \left(g_z \left(\frac{S_z}{S_{z,max}} \right) \right)^{\frac{1}{wz}}$$

$$\left(\sum_{z=1}^{Nz} W_z \right) = 1$$

where S_z is the observed value of stressor z in a micro-basin, $S_{z,max}$ is the maximum value of stressor z at the micro-basin level in the entire study area (where $S_z/S_{z,max}$ varies from 0 for unaltered to 1 for maximum impact), Nz is the number of stressors affecting the physical structure of the ecosystem, g_z is a mathematical function of a single variable that describes the degree of impact caused by stressor z, and W_z is the weighting factor. We used equal weights for each stressor with a value of $1/Nz$.

The stressors we refer to are anthropogenic disturbances that degrade ecosystems and, therefore, their functions (Flotemersch et al., 2016) (e.g., human-caused forest fires, agricultural land use, urban areas, and road density). To calculate the I_{PS} index, we used the stressors listed in Table 2. The technical details of the configuration, inputs, and outputs of the models used can be found in the Supplementary Material.

Connectivity: We constructed a longitudinal connectivity index (I_C):

$$I_C = \frac{L_B}{L_A}$$

where L_A is the length of the shortest path from a micro-basin to the mouth of the analyzed basin, without considering the presence of barriers that may generate a disconnection, and L_B is the length of the shortest connected path between a micro-basin and the mouth of the analyzed basin, considering the presence of barriers in the channel. In this case, the length is measured from the mouth to the first barrier encountered. Table 1 presents a summary of the integrity indexes by KEA. The implementation of the indexes described here (including scaling and ranges) is detailed in Step 3.12.

3.8 Models and analysis tools

To estimate the two groups of considered indexes—freshwater group indexes and river integrity indexes—we configured a set of models and analysis tools for each KEA. The purpose and objectives of these tools are outlined in the following sections. The Supplementary Material provides the technical details of the configuration, inputs, and outputs of the models.

3.8.1 KEA: Hydrological regime

We used the aggregated conceptual hydrological model GR4J (Perrin et al., 2003) to generate a time series of daily mean discharge in each of the micro-basins and sub-basins defined for the Caquetá River basin. We selected this model for its parsimonious structure, low data requirements for configuration, and good performance in tropical basins (Carvajal and Roldán, 2007; Anshuman et al., 2019; Carlos et al., 2023). For its configuration, we used data generated by the hydro-climatological monitoring network of the Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM), which consists of 104, 92, and 11 stations that record precipitation, temperature (maximum, minimum, and mean), and discharge, respectively. We used the Grubbs test (Grubbs, 1950), the Tukey test (Tukey, 1977), and the double median absolute deviation test (Prabhakar et al., 2022) to detect and remove outliers. We filled in missing precipitation and temperature records using the inverse distance weighting method (Shepard, 1968) and ordinary least squares method (Stahl et al., 2006), respectively. To calibrate the hydrological model, we applied the dynamically dimensioned search optimization algorithm proposed by Tolson and Shoemaker (2007) and selected the Nash-Sutcliffe efficiency coefficient as the objective function (Nash and Sutcliffe, 1970). The calibration and validation periods for the 11 selected discharge stations were 1985–2005 and 2005–2020, respectively.

To evaluate climate change, we relied on projected precipitation and temperature data between 2020 and 2050 from six global circulation models (Table 3). These data were generated under a shared socioeconomic pathway of fossil-fuel-driven development to reach a radiative forcing condition of 8.5 W/m^2 by 2,100 (most critical scenario) (Almazroui et al., 2021). We corrected bias in the data using the bias-corrected statistical disaggregation method (Wood et al., 2004; Gupta et al., 2019; Ratri et al., 2019). We used the adjusted series to run the GR4J model, generating six discharge series, which were then ensemble-averaged at each time step.

Using the toolbox for streamflow signatures in hydrology (Gnann et al., 2021) and the discharge series generated with the GR4J hydrological model for the historical condition, we assessed the selected hydrological signatures to determine the freshwater groups.

With the same tool, we constructed flow duration curves for both the historical and climate change conditions and calculated the hydrological integrity index, I_{HR}. The schematic representation of our calculation process for the two groups of hydrological regime indexes is shown in Supplementary Material.

3.8.2 KEA: Sediment transport

We used a modified version of the Catchment Sediment Connectivity and Delivery tool (Schmitt et al., 2016) to represent sediment flow and provenance in the Caquetá River basin. To configure the tool, we divided the micro-basins into those with sandy riverbeds and reaches with gravel beds, assuming that the former is capacity-limited (slope ≤0.025 m/m) and the latter are supply-limited (slope >0.025 m/m), using the criterion proposed by Flores et al. (2006).

We determined the bankfull hydraulic conditions (width, depth, and velocity) and the mean sediment size (D_{50}) by solving the equations proposed by Wilkerson and Parker (2011) (sand beds) and Parker et al. (2007) (gravel beds) based on the approach used by Schmitt et al. (2016). We verified the estimation results for micro-basins with sandy beds using D_{50} data from six sediment samplings we gathered from the main channel of the Orteguaza and Caquetá Rivers. The number of samplings was limited due to safety conditions in the Caquetá River basin. We adjusted both equations by introducing correction factors—one for slope in the sections with sandy beds and another for width in the channels with gravel beds—both of which depend on the bankfull discharge of the micro-basins.

We also adjusted the bankfull widths in sites with rapids or geological confinement using the rapid sites reported in the Instituto Geográfico Agustín Codazzi (2022) national base mapping and the corresponding 2020 satellite images from Google Earth. The bankfull discharge considered for the analysis corresponds to a 2.33-year return period. Finally, to calculate sediment transport, we used the equations by Engelund and Hansen (1967) and Wong and Parker (2006) for sections with sandy and gravel beds, respectively.

To calculate the contributions of suspended sediment, we used the InVEST sediment delivery ratio model (Natural Capital Project, 2022), which utilizes the revised universal soil loss equation (Renard et al., 1996) to estimate the annual amount of soil loss and, through the sediment delivery ratio (Vigiak et al., 2012a), estimates the proportion of soil loss reaching the river. For its configuration, we used the information presented in Table 4. We validated the simulated sediment delivery ratio values with the suspended sediment records reported by Instituto de Hidrología Meteorología y Estudios Ambientales (2019).

Once we configured the models, we used climate data, specifically the multi-year annual average precipitation and the bankfull discharge in the historical condition, to estimate the sediment transport capacity (an index for freshwater groups).

Similarly, we use climate data and discharge data associated with the flow duration percentiles of both the baseline and climate change scenarios to construct the sediment flow duration curve. Using the curve data, we estimated the integrity index I_{ST}. The Supplementary Material presents a schematic representation of our calculation of the two groups of sediment flow indexes.

3.8.3 KEA: Water quality

Based on the assimilation factor concept proposed by Chapra (2008), we constructed a steady-state water quality model that allowed us to estimate 14 water quality determinants (WQD) for the entire Caquetá River basin: temperature (T), conductivity (Co), organic nitrogen (NO), ammoniacal nitrogen (NH_4), nitrates (NO_3), organic phosphorus (Po), inorganic phosphorus (Pi), organic matter (MO), dissolved oxygen (O), suspended solids (SS), pathogenic organisms (X), elemental mercury (Hg^0), divalent mercury (Hg_2), and methyl mercury (MeHg). The equations for the assimilation

TABLE 3 CMIP6 global circulation models evaluated in the study.

Model	Institution	Country	Resolution
ACCESS-ESM1-5	Australian Community Climate and Earth System Simulator	Australia	1.25 ° × 1.875 °
CanESM5	Canadian Centre for Climate Modelling and Analysis	Canada	2.81 ° × 2.81 °
CESM2	National Center for Atmospheric Research	United States of America	0.9 ° × 1.25 °
EC-Earth3	Earth Consortium	Europe	0.35 ° × 0.35 °
MIROC 6	Japan Agency for Marine-Earth Science and Technology	Japan	1.4 ° × 1.4 °
MPI-ESM1-2-LR	Max Planck Institute for Meteorology	Germany	1.875 ° × 1.86 °

TABLE 4 Information used to configure the sediment delivery ratio in the Caquetá River basin.

Variable	Description
Precipitation	Fields interpolated with inverse distance weighting (Shepard, 1968) using the data fed into the hydrological model
Land use/land cover	2020 national land cover at a 1:100,000 scale generated by Instituto Amazónico de Investigaciones Científicas (2021)
Rainfall erosivity	Relationship proposed by Perez Arango and Mesa (2002) for Colombia
Soil erodibility	Method proposed by Anache et al. (2015), utilizing the textural distribution data from Hengl et al. (2017)
C coefficients	Values assigned in accordance with the information reported by Tosic et al. (2011), Rozos et al. (2013), Panagos et al. (2015), and Pacheco et al. (2019)
P coefficients	The default setting is 1 for all coverages

factors were derived from the ADZ-QUASAR water quality model (Lees et al., 1998), as addressed by Correa-Caselles (2022), Mamani (2022), Navas (2016), and Rojas (2011). The computational implementation of the assimilation factors was carried out in MATLAB using object-oriented programming. Our model was designed to operate at the topological network level under a recursive accumulation scheme, allowing us to analyze large topological networks in minutes with low memory consumption. Additionally, our model assimilates inputs from point and diffuse loads of different WQD.

Considering the identified agricultural sources of contamination (Table 1), we used the 2020 national coverages at a 1:100,000 scale generated by Instituto Amazónico de Investigaciones Científicas (2022b) to assign fertilization loads to crop areas. For fertilization with different forms of nitrogen, we assigned a fertilizer with proportions of 50% NO_3 and 50% NH_4. For grassland areas, we assigned organic fertilization (manure) with a proportion of 40% NO, 30% NO_3, and 30% NH_4 (Sociedad de Agricultores de Colombia, 2002). We obtained annual nitrogen load values per fertilizer from the British Survey of Fertiliser Practice (2018). For phosphorus, we assigned a fertilizer with a proportion of 70% Pi and 30% Po (Wade et al., 2007; Whitehead et al., 2011; Jackson-Blake et al., 2016), and we gathered annual phosphorus load values from Pérez-Vélez (2014). To estimate diffuse loads from livestock, we used information from bovine censuses (ICA, 2021) and the suggested loads by Iglesias-Martínez (1994). For coliform loads, we consulted Heras-Sierra et al. (2016). We used the connectivity index (Vigiak et al., 2012b) suggested in the Nutrient Delivery Ratio model (Natural Capital Project, 2022) to determine the proportion of nutrient delivery to the channel.

We gathered population data by population center (IGAC, 2022) from the National Population and Housing Census Departamento Administrativo Nacional de Estadística (2018) and presumptive loads for the WQD as defined by Ministerio de Vivienda Ciudad y Territorio (2017) for Colombia. For oil well concessions, we used data on producing oil wells reported by Agencia Nacional de Hidrocarburos (2022). For each well, we estimated the loads of the DWQ using the permissible discharge limits established by Ministerio de Ambiente Desarrollo Sostenible (2021). The quantities of water discharged per well were inferred from the water use factors for the production phases of hydrocarbons defined by Instituto de Hidrología Meteorología y Estudios Ambientales (2010). We quantified mercury discharges from legal and illegal gold mining using Colombia's gold production information for 2022 Unidad de Planeación Minero Energética (2022a) and the reported mercury use ratios by Diaz et al. (2020). To determine the distribution of the different forms of mercury, we used the proportions reported by Sanchéz and Cañon (2010) and previously implemented by Correa-Caselles (2022). The spatial distribution of the estimated mercury loads was performed using legally established mining titles (Unidad de Planeación Minero Energética, 2022b) and illegal mining sites reported by (RAISG, 2020). We validated the orders of magnitude of the modeled conventional determinants with data reported by Torres et al. (2021) and verified the mercury distributions with the results reported by Correa-Caselles (2022).

We used the modeled values of suspended solids, nutrients (nitrogen and phosphorus), and organic matter concentrations according to the ranges established by Maco-García (2006) to generate the attribute index for the freshwater groups (Table 1).

We adjusted the result with information on Amazonian water types developed by Ríos-Villamizar et al., 2013; Ríos-Villamizar et al., 2020a; Ríos-Villamizar et al., 2020b), Wildlife Conservation Society (2020), and expert opinions from professionals with extensive experience in the study area. Based on the results obtained from the model, we calculated the sub-indexes corresponding to each water quality determinant, which allowed us to estimate the integrity index I_{WQ}. In the Supplementary Material we present a schematic representation of the process we followed to calculate the two groups of water quality indexes.

3.8.4 KEA: Physical structure

For physical structure, we chose to use two indexes that do not require the construction of a mathematical model, diverging from the processes used for the previously described KEAs. Instead, we used an attribute-based approach for the freshwater group indexes and spatial analysis through stressor mapping to calculate the integrity index I_{PS} (Table 1).

Calculation of freshwater group indexes: We determined the degree of river confinement by evaluating the relationship between the width of the floodplain or active channel area (W_{ARA}) and the width of the bankfull channel (W_{bf}). According to Beechie et al. (2006), if $(W_{ARA}/W_{bf}) < 4$, the river is considered confined; otherwise, it is considered unconfined. We used the estimated values of W_{bf} and those configured with the Catchment Sediment Connectivity and Delivery tool and calculated the values of W_{ARA} using the Multi-Resolution Index of Valley Bottom Flatness (Gallant and Dowling, 2003) with a threshold of 1, which was coherent with the 2020 wetlands map of Colombia (Burbano-Girón et al., 2020).

Calculation of integrity index: Following the approach proposed by Flotemersch et al. (2016), we calculated the maximum value for each selected stressor per analysis unit. Considering that the Amazon's resilience is declining (Boulton et al., 2022), we assumed that the ecosystem response to stressors is one of low resilience. Therefore, we used a logistic function to represent the behavior shown by Flotemersch et al. (2016) and, in this way, estimated the I_{PS}. In the Supplementary Material, we present a schematic representation of our calculation for both groups of physical structure indexes.

3.8.5 KEA: Connectivity

By delimiting the micro-basins using a DEM, we obtained the river lengths between consecutive nodes or fluvial connections, which allowed us to define the topological relationships between the micro-basins using a graphical approach. From this information, the paths from each micro-basin to the mouth of the basin were calculated to construct the established attribute and integrity indexes (Table 1).

3.9 Freshwater groups

To identify the freshwater groups in the Caquetá River basin, we clustered the micro-basins based on the similarity of the KEAs using the indexes defined in Step 3.6 (Table 1). For this process, we used an agglomerative hierarchical clustering method and selected the inconsistency coefficient as the metric for determining the clusters (Saxena et al., 2017). During the clustering process, we categorized the indexes according to their ranges of variation, as shown in Table 5, and used these categories as the basis for clustering to define the freshwater groups.

3.10 Rarity index

We calculated the rarity (I_R) of a micro-basin belonging to freshwater group i as (Duarte et al., 2016):

$$I_R = -ln\left(\frac{a_i}{A}\right)$$

where a is the total area of the micro-basins belonging to freshwater group i, and A is:

$$A = \sum_{i=1}^{Ng} a_i$$

where Ng is the total number of freshwater groups. High values indicate a unique habitat in the basin, and low values indicate a common habitat. The Supplementary Material provides additional details for the rarity index calculation.

3.11 Connectivity index

To calculate the connectivity index, we constructed a directional upstream adjacency matrix (Wohl, 2017) that includes, for each unit, the degree of connectivity defined by the proximity between micro-basins, measured using the length of the main channel of each micro-basin. As an example, consider that the study area is segmented into five micro-basins, each of which has a river segment with a length of 5 km. The directional upstream adjacency matrix for the micro-basins would be represented by A. If we calculate the river segment lengths from one micro-basin to all upstream micro-basins, we obtain the matrix of accumulated distances, B. By estimating the maximum distance for each micro-basin, we obtain the matrix of maximum distances, C. The connectivity index (CI) would then be given by $1 - ((B_{(m,n)} - C_{(m,n)})/B_{(m,n)})$, where values near 1 indicate high connectivity and values close to 0 indicate low connectivity. The Supplementary Material offers additional details about the connectivity index calculation.

3.12 Integrity index

For the Caquetá River basin, we developed a global integrity index (I) for the micro-basins and sub-basins based on the integrity indexes (I_{ki}) selected for each KEA ($ki = HR, ST, WQ, PS, C$) in Step 3.7. We used a geometric aggregation method to integrate I_{ki} (Juwana et al., 2012; Thornbrugh et al., 2018). We assigned equal weights (w_{ki}) to all integrity indexes by KEA, considering that each is crucial for the integrity of freshwater ecosystems. Therefore, each I_{ki} was assigned a weight equal to $1/KI$, where KI is the number of KEAs selected in Step 3.5. The mathematical expression of I is:

TABLE 5 Ranges and values of attribute indexes per key ecological attribute (KEA) defined for the grouping of freshwater groups in the Caquetá River basin.

KEA	Name	Attribute index	Range	Description
Hydrology regimen	Mean annual flow (m^3/s)	1	0–10	Low flow river
		2	10–100	Medium flow river
		3	100–1,000	High flow river
		4	1,000–10,000	Very high flow river
	Slope of flow duration curve	1	−5.0–−2.4	Very high variability flow river
		2	−2.4–−1.8	High variability flow river
		3	−1.8–−1.19	Medium variability flow river
		4	−1.19–0.0	Low variability flow river
	High flow duration (months)	1	1.0–4.5	Low duration high flow
		2	4.5–5.5	Medium duration high flow
		3	5.5–6.5	High duration high flow
		4	6.5–7.5	Very high duration high flow
	Mean half flow date (months)	1	-	Average flow rate is reached in the first half of the year
		4	-	Average flow rate is reached in the second half of the year
	Frequency of peak flow	1	-	Single peak per year
		4	-	Two peaks per year
Sediment transport	Average sediment transport capacity, in bankfull condition (tons/year)	1	1.00E+00–1.00E+06	Low sediment transport capacity river
		2	1.00E+06–1.00E+08	Medium sediment transport capacity river
		3	1.00E+08–1.00E+10	High sediment transport capacity river
		4	1.00E+10–1.00E+15	Very high sediment transport capacity river
Water quality	Water types	1	-	Whitewater river
		2	-	Blackwater river
		3	-	Clearwater river, mountain
		4	-	Clearwater river, Amazon forest
Physical structure	Morphological configuration of river and sediment transport type	1	-	Confined, capacity-limited
		2	-	Unconfined, capacity-limited
		3	-	Confined, supply-limited
		4	-	Unconfined, supply-limited
Connectivity	Dendritic connectivity index (dimensionless)	1	0.00–0.25	Connected river, long distance
		2	0.25–0.50	Connected river, medium distance
		3	0.50–0.75	Connected river, small distance
		4	0.75–1.00	Connected river, very small distance

$$I = \prod_{ki=1}^{KI} I_{N_{ki}}^{\left(\frac{1}{w_{ki}}\right)}$$

$$I_{Nki} = \left(m^{*} I_{ki,r}\right) + \alpha_{r_{min}} - \left(m^{*}\, min\left\{I_{ki,r}\right\}\right)$$

$$m = \frac{\alpha_{r_{max}} - \alpha_{r_{min}}}{max\left\{I_{ki,r}\right\} - min\left\{I_{ki,r}\right\}}$$

In this equation, we normalize each I_{ki} using a linear scaling method. However, this normalization is performed differentially by range (r). The values of $\alpha_{r_{min}}$ and $\alpha_{r_{max}}$ correspond to the scaling limits used in each range: $min\{I_{ki,r}\}$ represents the minimum threshold of $I_{ki,r}$ in range r, and $max\{I_{ki,r}\}$ reflects the maximum threshold of I_{ki} in range r. In the end, I has values

TABLE 6 Scaling ranges of integrity indexes.

KEA	Range 1 $\alpha_{r\,min} = 0\ \alpha_{r\,max} = 0.25$	Range 2 $\alpha_{r\,min} = 0.25\alpha_{r\,max} = 0.5$	Range 3 $\alpha_{r\,min} = 0.5\ \alpha_{r\,max} = 0.75$	Range 3 $\alpha_{r\,min} = 0.75\ \alpha_{r\,max} = 1$
Hydrological regime	$0.15 > I_{HR}$	$0.15 \geq I_{HR} > 0.1$	$0.1 \geq I_{HR} > 0.05$	$0.05 \geq I_{HR} \geq 0$
Sediment transport	$0.15 > I_{ST}$	$0.15 \geq I_{ST} > 0.1$	$0.1 \geq I_{ST} > 0.05$	$0.05 \geq I_{ST} \geq 0$
Water quality	$0 \leq I_{WQ} \leq 0.5$	$0.5 < I_{WQ} \leq 0.7$	$0.7 < I_{WQ} \leq 0.9$	$0.9 < I_{WQ} \leq 1$
Physical structure	$0 \leq I_{PS} \leq 0.25$	$0.25 < I_{PS} \leq 0.5$	$0.5 < I_{PS} \leq 0.75$	$0.75 < I_{PS} \leq 1$
Connectivity	$0 \leq I_{C} \leq 0.25$	$0.25 < I_{C} \leq 0.5$	$0.5 < I_{C} \leq 0.75$	$0.75 < I_{C} \leq 1$

ranging from 0 to 1, where 1 reflects high integrity and 0 reflects low integrity. Table 6 presents the four ranges considered for the scaling of each I_{ki}.

The ranges used correspond to integrity index categories: low integrity $(0 \leq I < 0.25)$, medium integrity $(0.25 \leq I < 0.5)$, high integrity $(0.5 \leq I < 0.75)$, and very high integrity $(0.75 \leq I \leq 1)$.

3.13 Importance index

We constructed an importance index (I_{CV}) that groups v sub-indexes, which are estimated for each conservation value (CV_v) defined for the basin. This index ranges from 0 to 1, where a value of 1 represents units of high importance.

$$I_{CV} = \sum_{v=1}^{Ncv} CV_v$$

For fish, amphibians, reptiles, and waterbirds, we used the normalized values of the rarity-weighted richness index $(RWRI)$ (Williams et al., 1996; Abell et al., 2011). This index counts the number of species in a micro-basin and weights each species by the inverse of the number of micro-basins it occupies:

$$RWRI = \sum_{s=1}^{Sp_i} \frac{1}{N_s}$$

$$CV_{RWR} = \left(\frac{RWRI_i}{RWRI_{i,max}}\right)$$

where Sp_i is the number of species in micro-basin i, N_s is the total number of micro-basins occupied by species s, $RWRI_i$ is the observed value of $RWRI$ in micro-basin i, and $RWRI_{i,max}$ is the maximum $RWRI$ value in the entire study area.

For the remaining conservation values (see Table 7) we constructed a sub-index CV, where $X_{i,w}$ is the observed value of conservation value w in micro-basin i and $X_{w,max}$ is the maximum value of conservation value w recorded at the micro-basin level in the entire study area:

$$CV_w = \left(\frac{X_{i,w}}{X_{w,max}}\right)$$

Table 7 summarizes the sub-indices for the selected conservation values in the Caquetá River basin and presents the numerical ranges for each conservation value. Note that all values are scaled from 0 to 1 using the equation above. The Supplementary Material details the calculation of the conservation values sub-indexes.

3.14 Representativeness index

The representativeness index (I_{Rep}) of micro-basin i that belongs to freshwater group k is defined as:

$$I_{Rep} = \frac{1}{A_k}\left(\sum_{i=1}^{I} a_{k,w}\right)$$

$$A_k = \sum_{i=1}^{I} a_k$$

where $a_{k,w}$ is the area of micro-basins belonging to freshwater group k and contained within an existing conservation area w, and a_k is the area of all micro-basins belonging to freshwater group k (Duarte et al., 2016). The details of the representativeness index calculation can be reviewed in the Supplementary Material.

3.15 Complementarity criteria

To ensure complementarity in prioritization, we selected the areas of the natural parks as reported by Parques Nacionales Naturales de Colombia (2020). The Caquetá River basin currently contains 10 conservation areas representing 21% of the total area of the basin (Figure 2).

3.16 Definition of conservation opportunities

We used MATLAB Release 2019b to construct the 2D scatterplot of the Caquetá River basin to identify conservation opportunities. This platform allowed us to analyze and visualize the data and generate graphical outputs.

3.17 Prioritization

We solved the optimization problem for the Caquetá River basin by using the prioritizr package v8.0.2.1 (Hanson et al., 2023) to find an accurate, optimal solution in conjunction with Gurobi solver v10.0, which provides solvers based on integer linear programming. This combination of packages is computationally efficient compared with packages such as Marxan, which generates nearly optimal solutions (Beyer et al., 2016).

TABLE 7 Conservation values identified for the Caquetá River.

Category	Conservation values	Range
Species	Rarity-weighted richness index (fish, amphibians, reptiles, and aquatic birds)	0–0.02
	Number of species in danger of extinction	0–4
	Presence of migratory corridors	0 or 1
	Number of megafauna species	0–21
Ecosystem services	Distribution of person-days for recreation and tourism	0–1
Cultural areas	Presence of Indigenous reservations	0 or 1
	Presence of peasant reserves	0 or 1
	Presence of Raizal communities	0 or 1
Spiritual areas	Presence of sacred and spiritual sites	0 or 1

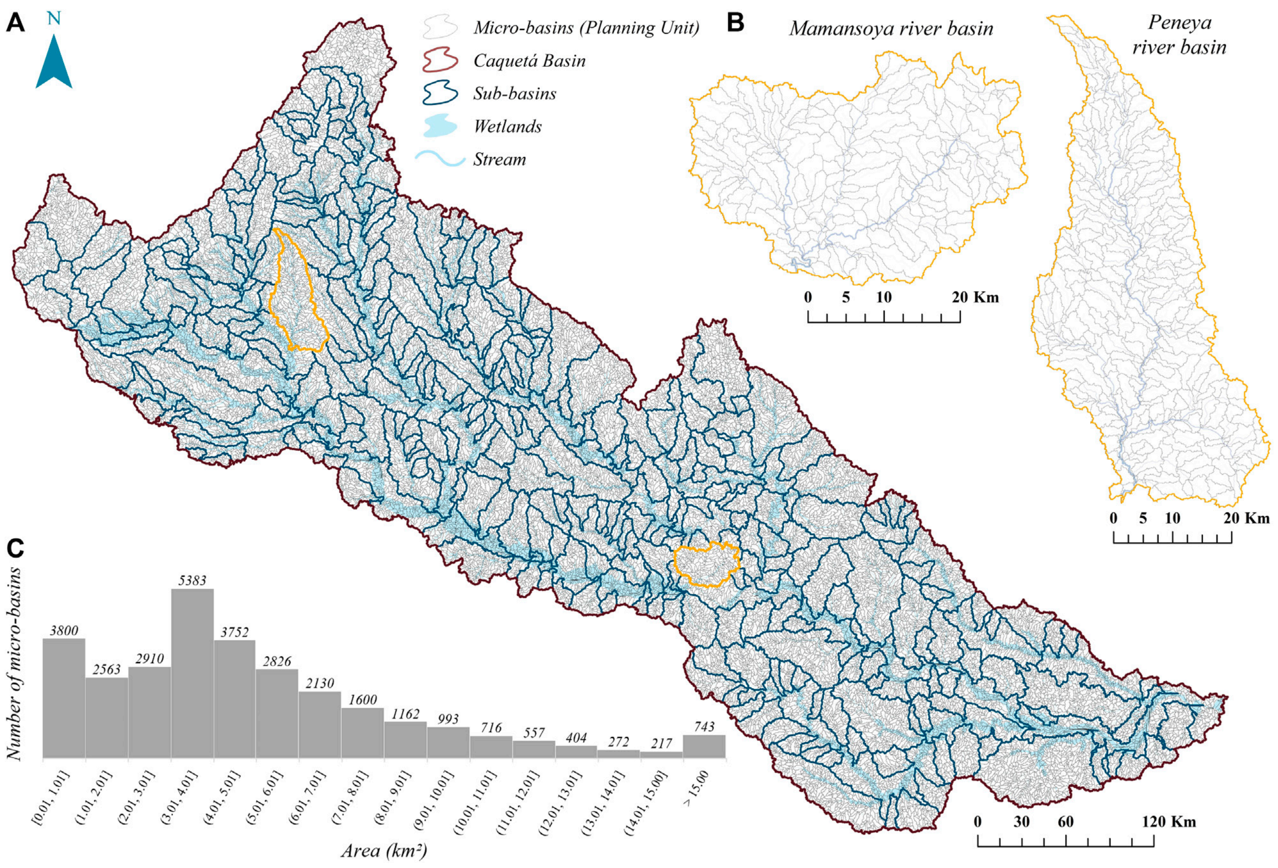

FIGURE 3
Caquetá River basin. **(A)** Spatial analysis units defined for the Caquetá River basin. **(B)** Distribution of micro-basins in the sub-basins of the Mansoya and Peneya Rivers. **(C)** Size frequencies of micro-basins.

4 Results

4.1 Spatial analysis units

Figure 3 presents the spatial units of analysis obtained for the Caquetá River basin. We delineated 30,028 micro-basins and 320 sub-basins for the study area (Figure 3A). Considering the large number of delimited micro-basins, Figure 3 shows example distributions of the micro-basins within the sub-basins of the Mamansoya and Peneya Rivers, located in the middle and upper part of the Caquetá River basin, respectively (see Figure 3B). Approximately 61% of the defined micro-basins are smaller than 5 km^2, and only 2.4% are larger than 15 km^2 (see Figure 3C).

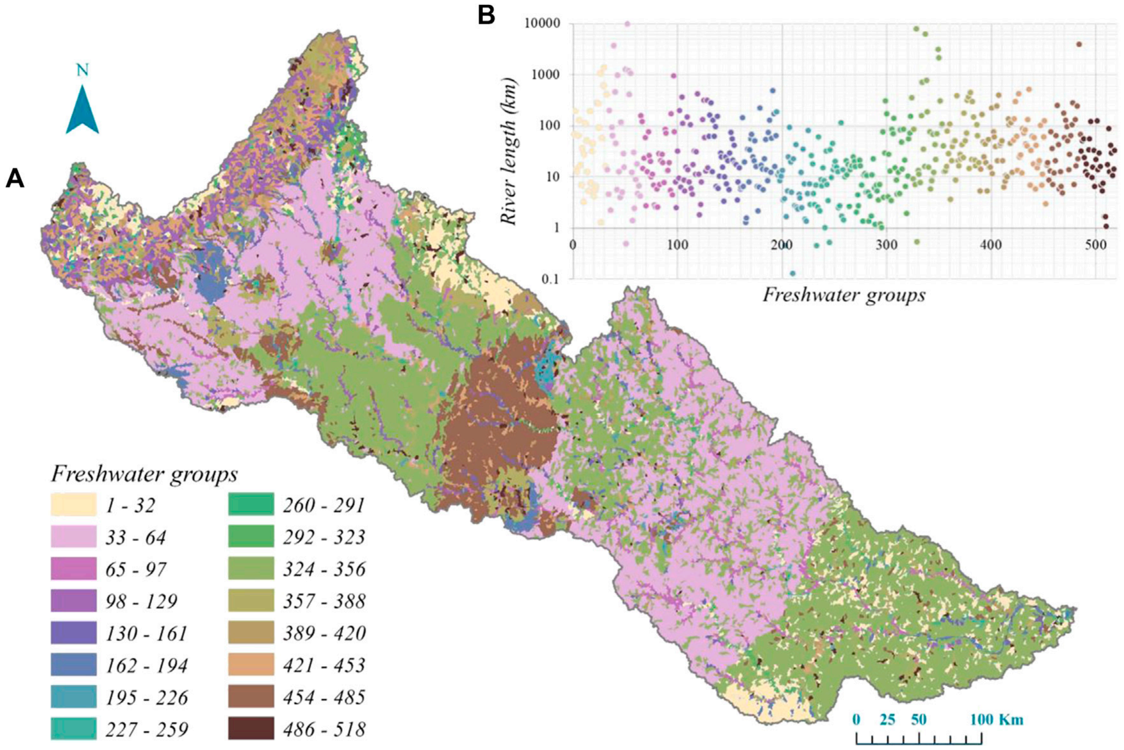

FIGURE 4
(A) Distribution of freshwater groups with unique key ecological attributes in the Caquetá River basin. **(B)** Length of rivers for freshwater groups.

4.2 Freshwater groups

We identified 518 freshwater groups with unique ecological characteristics (Figure 4); 28.4% of these are found in large and very large rivers (flow >100 m^3/s), and 71.6% are present in medium and small rivers (flow ≤ 100 m^3/s). Thirty percent of the identified groups are in the mountainous zone, which encompasses 11% of the entire Caquetá River basin. We also determined that 70% of the basin is occupied by only 4.2% of the identified freshwater groups.

4.3 Importance index

Figure 5A provides a spatial representation of the importance index in the Caquetá River basin, highlighting that the micro-basins that make up the main waterways were assigned the highest importance values. This is reasonable considering that these tributaries are migratory corridors for approximately 23 species of megafauna, including *S. fluviatilis* (He et al., 2018; 2021; Caldas et al., 2023), and other important species, such as *B. rousseauxii* (Córdoba et al., 2013). Moreover, the basin's structure does not currently contain river network interruptions.

High importance was assigned to the middle and lower zones of the Caquetá River basin, given the significant concentration of cultural values stemming from the presence of the Murui-Muinane, Yucuna, Andoque, Inga, and Coreguaje peoples (who occupy 43% of the entire basin area). These ethnic groups maintain a profound connection with the territory, as, in accordance with their worldview, they conceive the world as an entity encompassing the spiritual, material, and social dimensions. Consequently, they regard rivers as vital sources for their communities, providing them with sustenance through artisanal fishing and facilitating transportation within and beyond their territories (The Nature Conservancy and The Amazon Conservation Team, 2019). Additionally, areas of high importance were identified in the Andean region due to species abundance and the high provision of ecosystem-cultural services associated with recreation and tourism activities.

4.4 Representativeness and rarity indexes

We found that 46.7% of the identified freshwater groups in the Caquetá River basin are located within the 10 existing protected areas ($I_{Rep} > 0$). Of these areas, the Serranía de Chiribiquete National Natural Park stands out as it covers 13.1% of the entire basin area and hosts 23% of all identified groups, equivalent to 49.1% of the represented groups (Figure 5B, brown areas). We also discovered that 4.2% of the identified groups are considered rare (Figure 5C, red areas) because they are uniquely present within the basin. Out of these rare groups, 41% are found within protected areas. The representation levels of the identified groups are as follows: 29.8% have representation below 25%, 26% have representation between 25% and 50%, and 42.2% have representation above 50% (see Table 8).

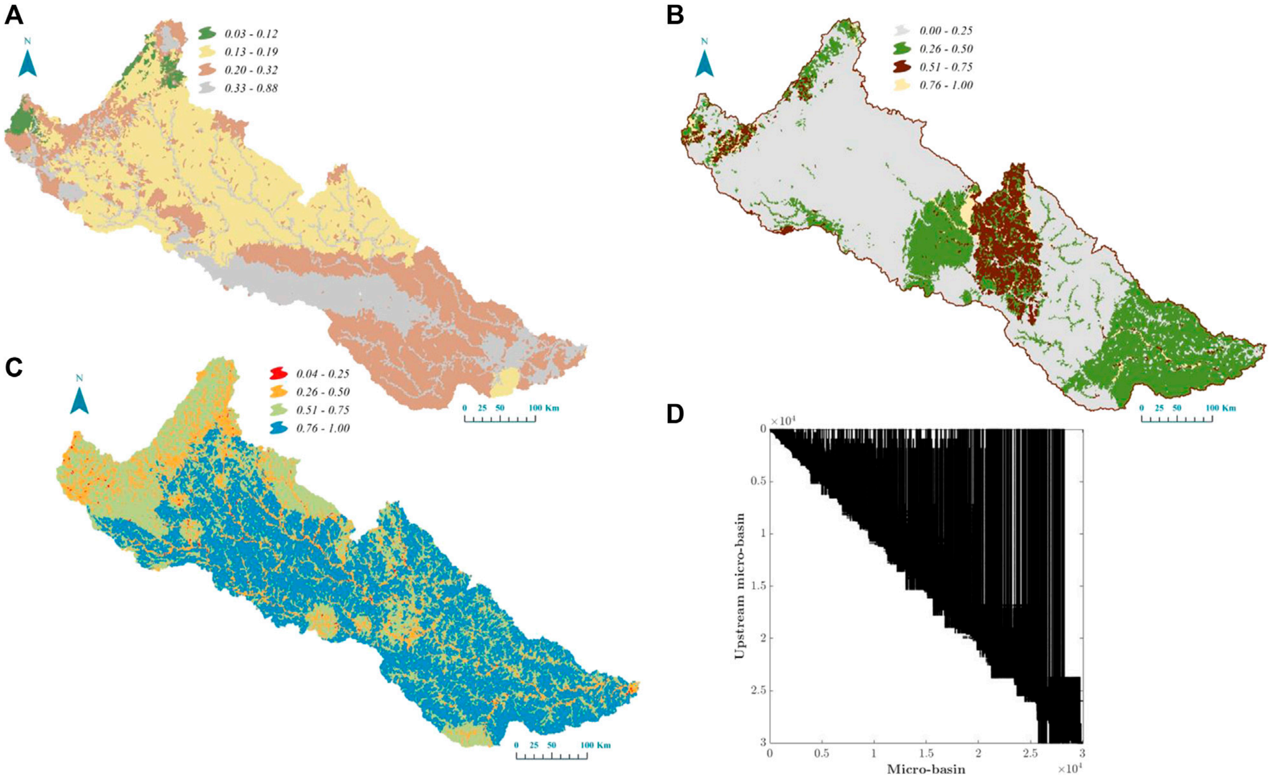

FIGURE 5
(A) Importance index. **(B)** Representativeness index. **(C)** Rarity index, and **(D)** Connectivity index.

4.5 Connectivity index

Figure 5D illustrates the graphical scheme of the connectivity index for the Caquetá River basin as an adjacency matrix. In this matrix, the asymmetry to the left indicates the direction of the connections between the micro-basins, showing the flow of water and interrelationships from the upper areas (upstream) to the lower areas (downstream).

4.6 Integrity

We found that 5.5% of the micro-basins presented low integrity values, 14.8% showed medium integrity values, 33.7% exhibited a high level of integrity, and 46% had a very high integrity rating (Figure 6A). The lowest integrity values were recorded in the upper part of the Caquetá River, especially in the Orteguaza and Caguán River basins (Figure 6A), which face the highest number of threats to the KEAs. Upon analyzing the integrity in the main channels of these rivers, we observed dispersed behavior with an increasing trend as the accumulated flow increases (Figure 6B), which translates into an increase in integrity downstream. However, in the lower part of the main channel of the Caquetá River, integrity values tend to decrease despite remaining high. Of the sub-basins, 1.7% had low integrity, 16.2% had moderate integrity, 33.4% exhibited high integrity, and 48.7% received a very high integrity rating (Figure 6C).

4.7 Conservation opportunities

The 2D scatterplot (Figure 6D) showed that the best opportunity to conserve 77.4% of the basins is through protection actions. This action shows a primarily continuous spatial pattern in the middle and lower zones of the basin, whereas the pattern is more scattered in the upper zone. Restoration presents a better opportunity in 4.7% of the basin, specifically in the upper, piedmont, and upper-middle zones. According to the integrity values, sustainable management should be implemented in 17.9% of the basin. The pattern of this action is primarily continuous and is present in the piedmont and upper-middle zones of the basin (Figure 6E). Furthermore, the results reveal that the established protection areas in the basin present the best opportunity for conservation, which we anticipated.

4.8 Prioritized portfolio

The spatial distribution of the prioritized portfolio is mainly concentrated in existing protected areas, specifically in the Serranía de Chiribiquete National Natural Park (Figure 7A), which is consistent with the selected criteria. The prioritized portfolio shows high connectivity between micro-basins, which generates corridors, as well as between existing protected areas. It is noteworthy that the prioritized portfolio includes the Caguán River despite its reduced integrity values in some sections. The portfolio managed to represent 96% of the freshwater groups

TABLE 8 Frequency distribution of rarity, representativeness, importance, and integrity indexes.

Rarity		Representativeness		Importance		Integrity	
I_R	Freshwater groups (%)	I_{Rep}	Freshwater groups (%)	I_{CV}	Micro-basins (%)	I	Micro-basins (%)
0–0.09	1.0%	0–0.1	59.1%	0–0.1	0.003%	0–0.08	10.9%
0.09–0.17	2.9%	0.1–0.2	4.8%	0.1–0.19	0.03%	0.08–0.17	25.9%
0.17–0.26	13.9%	0.2–0.3	5.8%	0.19–0.29	0.3%	0.17–0.25	14.6%
0.26–0.34	26.8%	0.3–0.4	4.4%	0.29–0.39	0.3%	0.25–0.34	15.0%
0.34–0.43	23.4%	0.4–0.5	6.4%	0.39–0.48	6.3%	0.34–0.42	11.3%
0.43–0.51	18.1%	0.5–0.6	2.5%	0.48–0.58	1.5%	0.42–0.5	4.7%
0.51–0.6	9.1%	0.6–0.7	3.3%	0.58–0.68	11.2%	0.5–0.59	5.0%
0.6–0.68	3.1%	0.7–0.8	1.9%	0.68–0.77	35.9%	0.59–0.67	5.4%
0.68–0.77	0.8%	0.8–0.9	1.7%	0.77–0.87	39.8%	0.67–0.76	4.8%
0.77–0.85	1.0%	0.9–1	10.0%	0.87–0.97	4.8%	0.76–0.84	2.5%

identified in the large and very large river categories and 74% of the freshwater groups identified in medium and small rivers. According to the defined conservation objective, the prioritized portfolio achieves representation of 80.1% of all the freshwater groups identified in the Caquetá River basin. We found that 91.9% of the prioritized micro-basins present opportunities for conservation through protection, 3% through restoration, and 5.1% through sustainable management (Figure 7B).

5 Discussion

In this study, we present a methodological framework that allows prioritization of freshwater ecosystems (micro-basins) and concurrently identifies the best conservation opportunities. The framework considers six criteria: representativeness, integrity, importance, rarity, complementarity, and connectivity. It is highly flexible in its configuration for each of the mentioned criteria. It has the capability to adapt to the specific characteristics of each region where it is to be applied, including modeling schemes and analytical tools for characterizing key ecological attributes, indexes, conservation values, data provided to establish criteria, and their relative weights.

The proposed framework contributes to improving the conservation strategies of freshwater ecosystems (challenge number 10, according to Olden et al., 2010). This approach goes beyond conventional SCP paradigms that prioritize areas based solely on unique or multiple species presence (Hermoso et al., 2018; Tognelli et al., 2019; Linke and Hermoso, 2022; Nogueira et al., 2023). For instance, the framework allows for the incorporation of critical elements for biodiversity maintenance and persistence, such as ecosystem services and cultural values, emerging as crucial factors to ensure effective long-term conservation (Higgins et al., 2021). The integration of culturally relevant values for communities becomes critically important as it facilitates understanding and acceptance of conservation actions, in addition to enhancing community engagement by ensuring appropriate representation.

As detailed in step 2.17, the prioritization scheme (optimization) was set up so that micro-basins of greater significance (with lower conservation value occurrences) are prioritized first, while those of lesser significance are relegated, regardless of the level of overlap in feature distributions (freshwater groups). This suggests that micro-basins with high ecosystem service provision and a high concentration of cultural values could be prioritized first, even if they have a low biological value. Such an outcome is consistent within our framework since it focuses on freshwater ecosystems and not on a specific species.

Within the framework, it is possible to incorporate a variety of conservation values into the significance criterion. In the specific context of the Caquetá river basin, our consideration encompassed recreation and tourism as cultural ecosystem services. However, this importance index has the potential for expansion to include provisioning, supporting, and regulating ecosystem services; or to cover other forms of cultural values beyond the scope of this study. Nonetheless, depending on the quantity, configuration, and weighting given to conservation values, the spatial distribution of prioritized micro-basins may shift. Yet, considering that cultural and social values are related to areas of biological importance, it would be expected that this variation would not be significant, as evidenced by Whitehead et al. (2014) in terrestrial ecosystems.

Integrating cultural relevant values for communities is essential for enhancing SCP as it facilitates the understanding and acceptance of conservation actions, in addition to bolstering community participation, which in turn increases the likelihood of success of these actions (Geist, 2015; Corrigan et al., 2018; Hoffmann, 2022). Furthermore, incorporating ecosystem services into conservation strategy formulation allows for the design of financial mechanisms grounded in these services (Boulton et al., 2016), such as recreation and tourism. These approaches motivate communities to conserve freshwater ecosystems. The inclusion of these elements not only aids in devising more effective conservation strategies but also establishes robust funding sources that support the long-term protection of ecosystems.

The integration of connectivity in SCP exercises has been highlighted as a key criterion for the conservation of freshwater

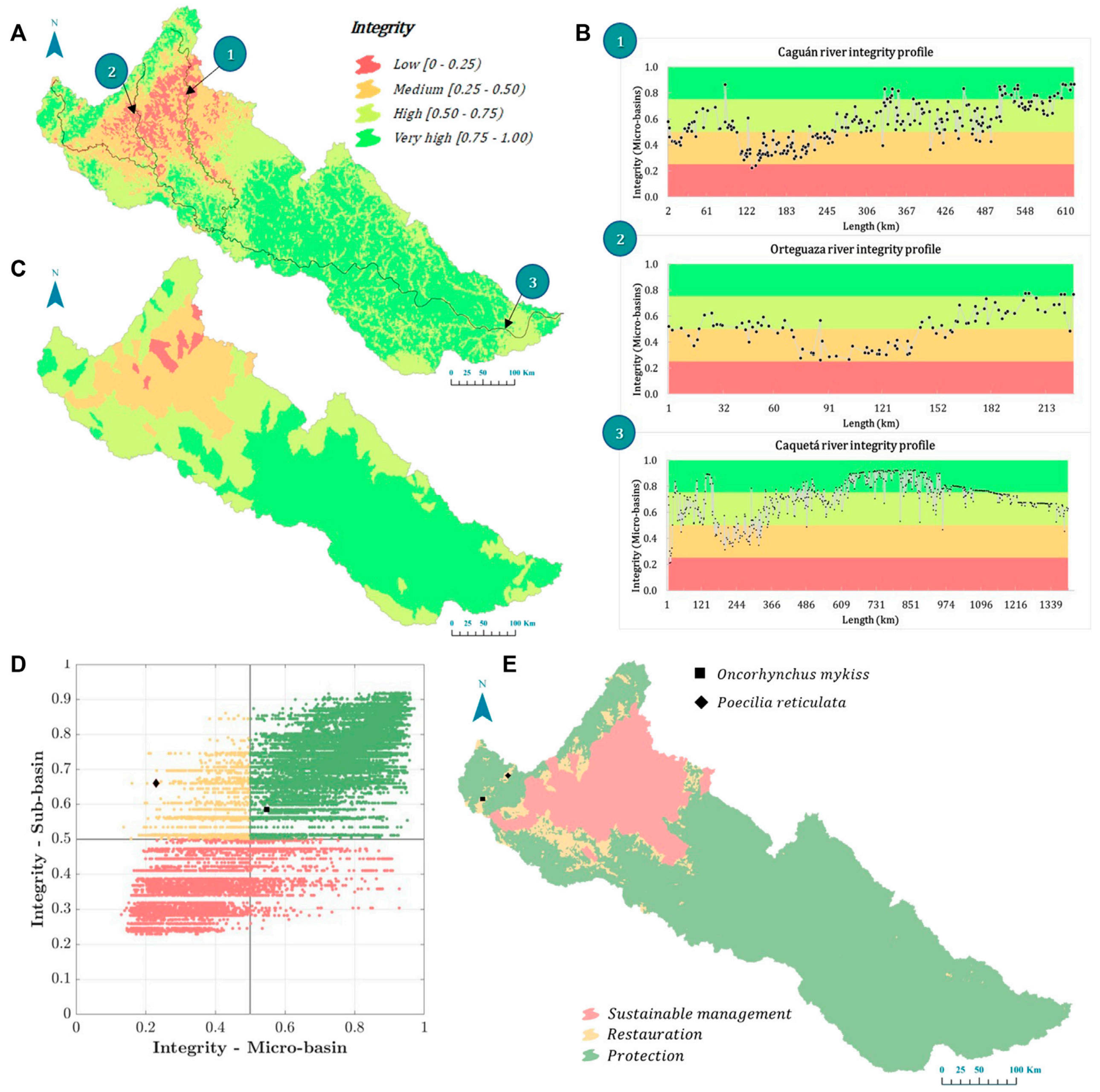

FIGURE 6
(A) Integrity at the micro-basin level. **(B)** Integrity profile of the Caquetá, Orteguaza, and Caguán Rivers at the micro-basin level, starting from their headwaters. **(C)** Integrity at the sub-basin level; **(D)** 2D scatterplot following Riato et al. (2020). **(E)** Conservation opportunities. The black diamond and square denote the presence of invasive alien species.

ecosystems, given their interconnected nature (Hermoso et al., 2011). Consequently, it has been increasingly incorporated into SCP frameworks (Linke and Hermoso, 2022; Nogueira et al., 2023). In our framework, connectivity is addressed not only as a desirable characteristic in the conservation portfolio but also as an attribute for defining freshwater groups and assessing their integrity. This, in turn, impacts the selection of conservation opportunities and the prioritization process.

Another significant aspect of our framework is that representativeness and rarity are properly directed towards freshwater groups, recognizing that KEAs shape and organize the physical habitat and biotic communities of freshwater ecosystems (Poff et al., 1997; Castello et al., 2013; Zeiringer et al., 2018; Higgins et al., 2021). Therefore, our approach aims to prioritize micro-basins with differentiated KEAs (freshwater groups) that are not yet represented in a protected area and are unique within the basin. It also takes into account the pressures to which freshwater groups are exposed through the integrity criterion. Although we favor healthy (high-integrity) ecosystems and those with high conservation values, this does not preclude the selection of areas

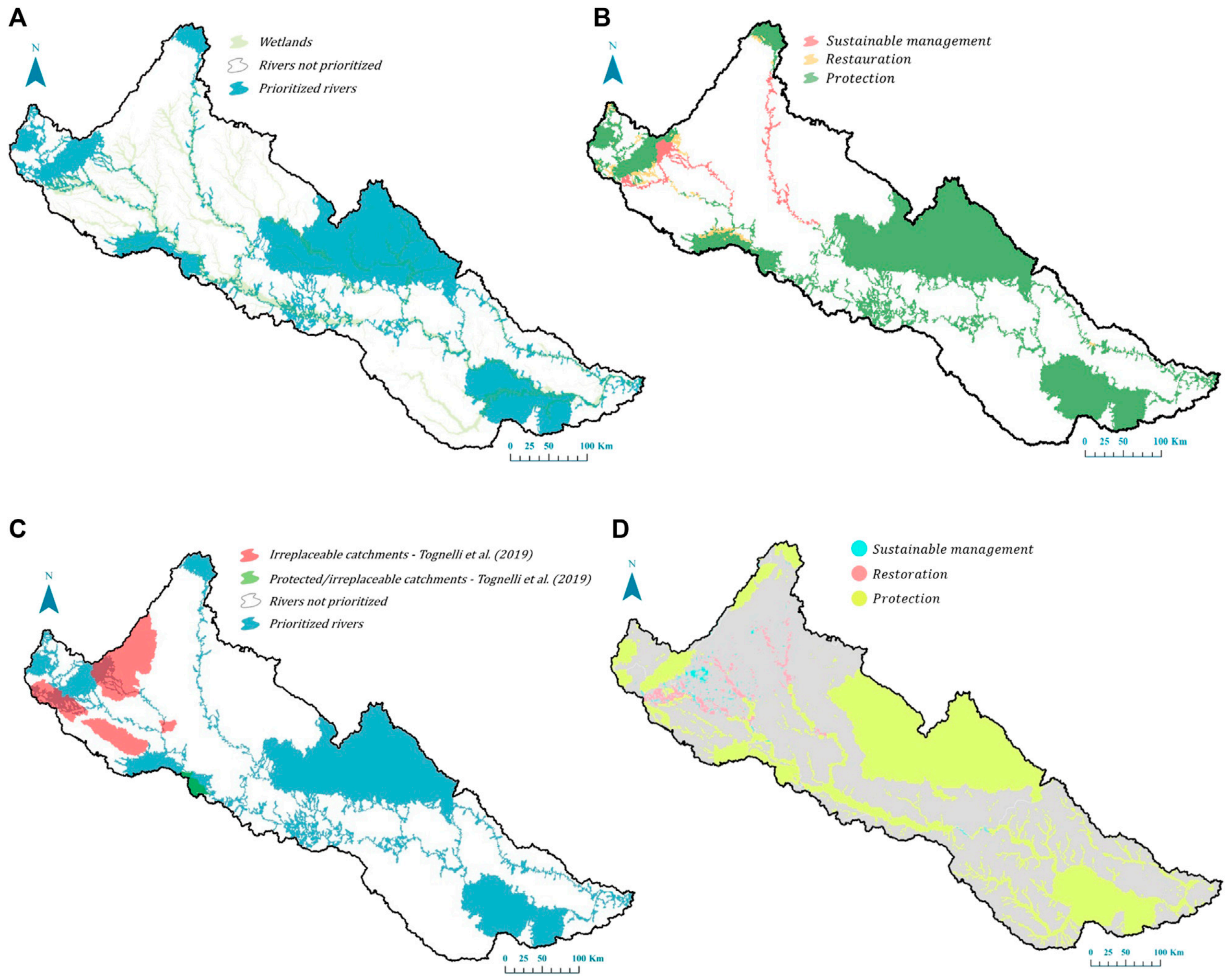

FIGURE 7
(A) Prioritized portfolio for the Caquetá River basin and **(B)** conservation opportunities for the prioritized areas. **(C)** Comparison of the prioritized portfolio with the sites identified by Tognelli et al. (2019) and **(D)** the Essential Life Support Areas in Colombia mapped by Corzo et al. (2021).

with low integrity as long as the greatest diversity of freshwater ecosystems is guaranteed, according to the proposed goal. In the case of the Caquetá River, we achieved a high representation of ecosystems with differentiated KEAs in the prioritized portfolio even though the search margin was limited to less than 11% of the area of the micro-basins in the Caquetá basin, considering that 21% of the Caquetá basin is currently under protection.

Our prioritized portfolio results (Figure 7A) in the Andean zone of the upper Caquetá River, upper Orteguaza River basin, and between the mouth of the Orteguaza River and the Caguán River, show agreement with the irreplaceable conservation areas identified by Tognelli et al. (2019) for freshwater fishes in the tropical Andes region of South America, threatened and vulnerable to climate change (Figure 7C). This alignment is attributed to our methodological framework's primary criterion, emphasizing endemic and threatened fish species. However, disparities are noticeable in specific regions, stemming from Tognelli et al. (2019) utilization of a traditional CPS scheme with Marxan, centered on individual species, while our approach is specifically tailored to freshwater ecosystems. Notably, Tognelli et al. (2019) did not account for rarity, ecosystem services, and cultural values in their assessments.

Furthermore, Tognelli et al. (2019) incorporated Marxan's Boundary Length Modifier (BLM) to derive interconnected solutions. However, their methodology did not encompass an evaluation of longitudinal connectivity, leaving room for future extensions in research. Consequently, the solution proposed by Tognelli et al. (2019) does not delineate areas forming connected basin corridors, which is a significant distinction from our approach.

Our conservation opportunity results (Figure 7B) are very similar to the Essential Life Support Areas (ELSA) mapped by Corzo et al. (2021) for Colombia following the United Nations Convention on Biological Diversity, Framework Convention on Climate Change, and Sustainable Development Goals (Figure 7D). ELSA identifies regions for conservation, restoration, and sustainable management through land use zoning, leveraging environmental diagnostics and assessments of environmental supply and demand. This methodology involves evaluating anthropogenic pressures affecting the given territory. In our study, we conducted an integrity analysis within our methodological framework, which corresponds to the approach taken by ELSA. However, it is important to note that ELSA incorporates aspects of public policy that are not integrated into our framework, leading to variations in proposed conservation activities across certain regions.

The identification of protected areas has been another focus of SCP analysis (Dorji et al., 2020; Hermoso et al., 2011; Linke & Hermoso). Instead of considering protection as the lone conservation option, our methodology applies the framework of Riato et al. (2020) and assesses the integrity of KEAs according to their threats to generate micro-basin-level spatial guidance regarding which ecosystems should be conserved using protection, restoration, or sustainable management. In the case of the Caquetá River basin, sustainable management and restoration opportunities were identified in sites with land overuse compared with the predominant vocation, e.g., due to productive activities such as livestock and agriculture (Guerrero, 2020). Protection, on the other hand, prevailed in some areas of the basin lacking strong anthropic pressures.

In certain regions, mercury contamination is a growing threat due to illegal gold mining (Matapí, 2015; Instituto Amazónico de Investigaciones Científicas, 2022b), which, in the future, could change the patterns of conservation opportunities for restoration, especially in the Caquetá River's main channel. This result is consistent with the findings of Corzo et al. (2021), who analyzed 100 geographic layers from 18 different institutions to identify conservation opportunities. Thus, a simple approach, such as that used by Riato et al. (2020) can i) allow conservation managers to determine specific actions according to each ecosystem's threats and capacity to support such actions (Riato et al., 2020; 2023) and ii) guide detailed exercises for resource allocation, as in Cattarino et al. (2015) and Mu et al. (2022).

Using an index-based approach, our proposal can link additional criteria to those presented in this research. Moreover, we have identified an opportunity for improvement in our methodology: we can include a KEA that specifically addresses biotic interactions and thus develop an index that adequately captures these processes. This will allow us to broaden the understanding of ecological and biological aspects within our approach, providing a more complete view of freshwater systems and how to conserve them. These interactions are crucial for maintaining natural diversity and ecological processes and understanding the dynamics of the distribution and abundance of freshwater species, especially in the presence of exotic invasive species that pose a threat to aquatic ecosystems (Castello et al., 2013; Zeiringer et al., 2018).

A recent study by Nogueira et al. (2023) demonstrated that relying solely on species presence data may be insufficient to address ecological needs. The presence of two invasive exotic species, *Oncorhynchus mykiss* (rainbow trout) and *Poecilia reticulata* (guppy), has been recorded in the Villalobos and Mocoa Rivers, located in the upper part of the Caquetá River basin. These invasive species are found in micro-basins where we identified restoration and protection as the best conservation opportunities (Figure 6). The presence of these species has significant implications for restoration processes, from both ecological and social perspectives. Actions such as eradication and control can involve the community capturing and consuming these species, generating social, economic, and environmental benefits. We, therefore, advise incorporating an index that highlights biotic interactions, thus expanding the specific measures related to these interactions.

There are multiple challenges involved in the implementation of the Convention on Biological Diversity (Chandra and Idrisova, 2011), especially for the 30 × 30 target, including Indigenous issues or the increasing degradation rate of ecosystem services (Chandra and Idrisova, 2011). According to the analyses conducted by Moreno et al. (2020), Indigenous reserves are vulnerable to ecosystem degradation processes. In the case of the Caquetá River basin, 43% of the basin's area corresponds to Indigenous reserves (Agencia Nacional de Tierras, 2023), and our results show that these areas are good candidates for conservation. Promoting environmental governance in Indigenous reserves is fundamental to reducing biodiversity loss in the Amazon (Moreno et al., 2020). This highlights the importance of our contribution, as our methodology considers Indigenous communities and their cultural values. This step forward will allow for the development and long-term sustainability of conservation strategies, especially in Amazonian basins, such as the Caquetá River, where Indigenous communities have an important presence.

6 Conclusion

In this study, we present a methodological scheme of SCP for freshwater ecosystems that simultaneously answers the questions of where and how to conserve. Our framework considers basins as planning units; incorporates integrity from the perspective of the functional characteristics of the ecosystem as a criterion for prioritization and selection of conservation opportunities; assesses the impact of threats to ecosystems; includes species, ecosystem services, and cultural and spiritual values as conservation values; considers existing conservation efforts; and recognizes the unique components and connectivity of freshwater ecosystems.

The proposed framework provides a pertinent technical instrument for optimizing the interventions of conservation organizations and, in turn, assisting Colombia in achieving its 30 × 30 target set by the Convention on Biological Diversity. By identifying priority freshwater ecosystems in the Caquetá River basin, we offer a tangible foundation upon which future decisive conservation actions in the Colombia can be based. Although our framework suggests an integrative capacity at the national level, it is crucial that subsequent research strengthens and broadens these findings. In summary, the defined methodological framework stands as an essential tool for decision-making regarding conservation, especially when considering ethnocultural territorial contexts.

The research community must continue to generate methodological frameworks in which SCP exercises of freshwater ecosystems incorporate conservation actions into the portfolios. We also encourage researchers to further strengthen our proposed methodological framework by analyzing how KEAs and biotic structure/composition respond to threats while also constructing and incorporating new KEAs, conservation values, and indexes that capture synergistic components at local scales and cumulative impacts at the basin level. In addition, we believe that our framework can be adapted to other geographies and scales of analysis, so we encourage future studies to corroborate this.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

JN: Conceptualization, Data curation, Methodology, Writing–original draft, Writing–review and editing. CR-P: Conceptualization, Methodology, Writing–review and editing. MC: Data curation, Writing–review and editing. AV-L: Methodology, Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Dietary flexibility of western red colobus in two protected areas with contrasting anthropogenic pressure

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Food distribution and abundance can affect intra- and inter-dietary variation in non-human primates, influencing feeding ecology and altering behaviour. Natural and/or human-induced actions can influence the dynamics between primates and the environment, with associated impacts on socio-ecology and demography. This relationship in anthropogenic landscapes, however, is poorly understood. Here, we use DNA metabarcoding to obtain high resolution dietary diversity data, and multivariate generalised linear models to investigate variation in the diet of this threatened primate. We characterise the diet of the western red colobus (*Piliocolobus badius*) in both the better preserved Gola Rainforest National Park (GRNP, Sierra Leone), and in the fragmented forests of Cantanhez National Park (CNP, Guinea-Bissau), and evaluate biological, ecological and temporal differences. Dietary plant species richness was high in both protected areas, and the type of plants consumed varied significantly across seasons, space, and time. Although we identify dependence on a few key plants, red colobus in CNP consumed a higher average number of plant taxa than in GRNP, and 11% of the diet consisted of cultivated foods (e.g. mango). This is the first time a molecular approach has been used to investigate red colobus diet, and reveal dietary flexibility in degraded forests.

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Predicting the consequences of dietary change on long-term population persistence, however, remains a significant knowledge gap. Nevertheless, our results provide critical information to inform targeted regional conservation planning and implementation.

KEYWORDS

non-human primates, feeding ecology, DNA metabarcoding, non-invasive sampling, west Africa, *Piliocolobus badius*, altered habitats

1 Introduction

The feeding ecology of non-human primates (hereafter primates) is driven by a dynamic relationship between the primate itself and its environment, with responses linked to morphology and physiology (Robbins and Hohmann, 2006). Most primate species live in tropical forests, where clear seasonal variation in rainfall, temperature, photoperiod, and phenology (van Schaik et al., 1993; van Schaik and Brockman, 2005; van Schaik and Pfannes, 2005) forces adaptation to spatial and temporal variation in food resources (Ma et al., 2017). Food distribution and abundance can strongly influence primate density, population dynamics, activity budgets, and relationships between individuals (Chapman et al., 2004; van Schaik and Brockman, 2005; Marshall and Leighton, 2006). Indeed, inter- and intra-species variation in dietary profiles is commonly observed, even among neighbouring groups of the same population occupying different home ranges. Time budgets can be adjusted for feeding, resting, travelling and in social behaviour, as in the case of a red colobus (*Piliocolobus kirkii*) group living in a habitat rich in herbaceous plants; this low-quality plant type was a large proportion of the diet, especially when tree foods were scarce, and individuals spent less time moving, and more time grooming and in aggressive interactions, than the forest group living in an area where tree foods were more available (Siex, 2003). Primate food selection and avoidance is linked to several causal factors, but it can only be a successful strategy if the nutritional requirements of the forager can be fulfilled with sufficient energy and other nutrients from the items of choice (Oftedal, 1991). In some cases, primates can shift diets to less preferred items, or complement it with cultivated items which are palatable, energy-rich and easily digestible (Naughton-Treves et al., 1998; Hockings and McLennan, 2012).

Natural variation in vegetation composition can negatively impact some primate populations, while others can thrive in subsequent forest regeneration events (Isabirye-Basuta and Lwanga, 2008). In the Anthropocene, however, humans (*Homo sapiens*) are a hyperkeystone species that can exert direct or indirect ecological impacts on other keystone species across different ecosystems (Worm and Paine, 2016). These changes may occur at a faster rate, more frequently and/or at a larger scale, and little is known about primate resilience to such alterations. Varying levels of habitat disturbance suggest differential flexibility among primate species and populations, and some may be unable to adapt to fast-changing environments (Onderdonk and Chapman, 2000; Isabirye-Basuta and Lwanga, 2008; Struhsaker, 2010; Dunham, 2017). A growing evidence base on primate behavioural flexibility and adaptation to forest fragmentation and anthropogenic habitats (Henle et al., 2004) shows that not all species are in decline, and some have higher resilience than expected. Primates exhibit behavioural and dietary flexibility to the environment in various forms, but dietary adjustments are the most frequently reported in the literature (McLennan et al., 2017).

Despite dietary and behavioural flexibility, some primates are highly vulnerable to tropical forest loss, degradation and ecosystem change, particularly arboreal or forest-dependent species (Isaac and Cowlishaw, 2004). A global meta-analysis showed negative impacts of anthropogenic habitat modification on primate communities and assemblages, potentially driving drastic population declines (Almeida-Rocha et al., 2017). Recently, populations of south American primates that appeared to sustain adaptive potential and resilience in reduced and fragmented habitats, were shown to experience limitations at the population level (see examples in Strier, 2021). Individual behavioural and dietary flexibility in howler monkeys (*Allouata* spp.) can mask limited post-disturbance recovery capacity at the population level, such as yellow fever outbreaks linked to local extinctions (Bicca-Marques et al., 2020). These and other factors operating at the ecological and biological levels (e.g. restricted gene flow among isolated populations in fragmented forests, reduced genetic diversity and increased vulnerability to stochastic events, such as natural disasters and disease) can determine the capacity for survival in altered environments. Understanding ecological and behavioural responses to human-induced changes in primate habitats is an urgent challenge given the growing number of primate populations living in closer contact with human populations (Estrada et al., 2020).

Analysis of plant and animal items in primate diet has traditionally required direct observations of feeding behaviour, and/or macro- or microscopic identification of digested food remains from stomach content or faecal samples. These methodologies require extensive observations, long distances to follow the groups, and preferentially habituated primates (Doran-Sheehy et al., 2006). Furthermore, data quality often depends on researcher expertise, and the type of habitat inhabited by the focal primate (e.g. it is harder to observe feeding events in higher and denser canopy) (Struhsaker, 2010). Moreover, taxonomic identification of food items is challenging, as highly digested plant remains in faeces can be indistinguishable. Hence, a molecular approach using DNA metabarcoding of items ingested by primates, has the potential to provide a more accurate and exhaustive analysis of diet composition (Pompanon et al., 2012; Taberlet et al., 2012). This technique allows for rapid identification of multiple taxa in a single experiment by combining DNA taxonomy and high-throughput sequencing (Coissac et al., 2012; Pompanon et al., 2012; Ji et al., 2013). By amplifying one or more targeted DNA sequences that exhibit consistent differences between taxa and are highly variable, it is possible to identify plants and animals against taxonomic reference databases of the organisms in question. This has been a successful alternative to more traditional approaches across many taxa, elucidating the dietary diversity of elusive species, and revealing rare prey items (Ait Baamrane et al., 2012; Lyke et al., 2019; Schmack et al., 2021; Querejeta et al., 2020).

Colobinae, a subfamily of the Old-World monkey family (species of Africa and Asia), are both arboreal and an easy target for commercial and subsistence hunting (Linder et al., 2021), rendering them particularly vulnerable to habitat alterations. Colobine monkeys have a complex evolutionary history, resulting in distinct anatomy, ecology and social dynamics (Ting, 2008; Linder et al., 2021). They differ from all other cercopithecines, and generally from other primates, with a large, multi-chambered stomach, a specialised gut microbiome, enlarged salivary glands and high-cusped molar teeth (Davies and Oates, 1994). These adaptations enable exploration and subsistence on difficult to digest, low-quality food items (Oates and Nash, 2011; Fleagle, 2013). Early studies identified colobines as leaf-eating monkeys (Davies and Oates, 1994), requiring the protein and fibre content of foods. However, later research showed that colobus monkeys, including red colobus (*Piliocolobus* spp.), feed mainly on leaf buds, flowers or immature seeds and fruits from a diverse range of plant species, using mature leaves when preferred food is scarce (Maisels et al., 1994; Oates, 1994; Koenig and Borries, 2001). Diversity is maintained throughout the year and appears not to correlate significantly with ripe fruit availability (Conklin-Brittain et al., 1998; Wrangham et al., 1998; Chapman et al., 1999). Like other primates, *Piliocolobus* species supplement its diet with nutritious and easily digestible food items (Mowry et al., 1996; Chapman and Chapman, 2002). In some cases, such foods are simply other plant parts or arthropods, but in more degraded habitats, cultivated species are also consumed (Galat-Luong and Galat, 2005; van Schaik and Brockman, 2005). The ashy red colobus (*tephrosceles*), for example, included cultivated bean seeds in the diet (Kibaja, 2014).

Research on red colobus feeding ecology has mainly focused on east rather than west African species. The western red colobus (*Piliocolobus badius*) occurs from Senegal to Côte d'Ivoire and is currently listed by IUCN Red List as Endangered (McGraw et al., 2020), due to habitat loss, degradation and fragmentation associated with global and local demand for natural resources, commercial and subsistence hunting (McGraw et al., 2020), and increased exposure to predators and infectious diseases transferred from humans and domesticated animals (Galat-Luong and Galat, 2005; Hillyer et al., 2015; Düx et al., 2017). This species occurs in two National Parks: Gola rainforest in Sierra Leone (GRNP), and Cantanhez in Guinea-Bissau (CNP); despite having small populations (5,000 individuals in GRNP, Linder et al., 2021; and < 500 individuals for an effective population size in CNP, Minhós et al., 2016), the red colobus conservation action plan for 2021–2026 identifies the two protected habitats as key areas for conservation (Linder et al., 2021). No dietary studies have been conducted for either population, but in a scan sampling of habituated *badius* of Tiwai Island Wildlife Sanctuary, southwest of GRNP (Figure 1), nearly half of the annual diet consisted of non-foliar items: seeds, young leaves, and mature leaf parts contributed to 73% of the species diet complemented with a high intake of whole fruits and flowers (Davies et al., 1999). Gathering evidence on dietary flexibility for populations exposed to different habitat threats is therefore crucial for the long-term conservation of this species.

In this study we aim to investigate the diet of western red colobus in two protected areas (PAs) in west Africa, with distinct anthropogenic and landscape characteristics. Using the UniPant specific primer (Moorhouse-Gann et al., 2018) to amplify the DNA of ingested plants, we can compare the diet of the red colobus population inhabiting the highly fragmented and anthropogenic landscape of CNP in Guinea-Bissau, with the population inhabiting one of the largest and well preserved west African forest, the GRNP in Sierra Leone. We investigate spatial and temporal dietary variations of western red colobus populations in each PA by i) characterising the diet and determining species richness; ii) describing local seasonal variation; iii) identifying putative sex, spatial and temporal differences; and iv) describing the species dietary flexibility in each landscape. Reflecting primate behaviour, we expect to observe intraspecific dietary variation across seasons in both PAs, but a lower plant richness, narrower niche breadth and higher presence of cultivated food items in the diet of the population inhabiting the more degraded habitat (CNP) than the more connected and protected forest of GRNP.

2 Materials and methods

2.1 Study areas

Our study focused on two PAs in west African countries, Guinea-Bissau and Sierra Leone (Figure 1), within the African wet tropical climate zone that supports some of the most biodiverse tropical forests in west Africa (White, 1983; Myers et al., 2000). Rainfall in both PAs is highest between May and November (rainy season), with a dry season from December to April. Most plant species in both PAs have one or two foliage peaks, with species-specific timings that allow young leaves to be present throughout most of the year (Oates, 1988; Bessa, 2014). Detailed information on forest types and common plants present in each PA can be found in Supplementary Tables S1, S2. Gola Rainforest National Park (GRNP), southeast Sierra Leone, comprises approximately 750 km^2 of three largely intact rainforest blocks (Gola north, central and south). This PA is dominated by trees in the mature forest, with some areas of secondary forest and regrowth

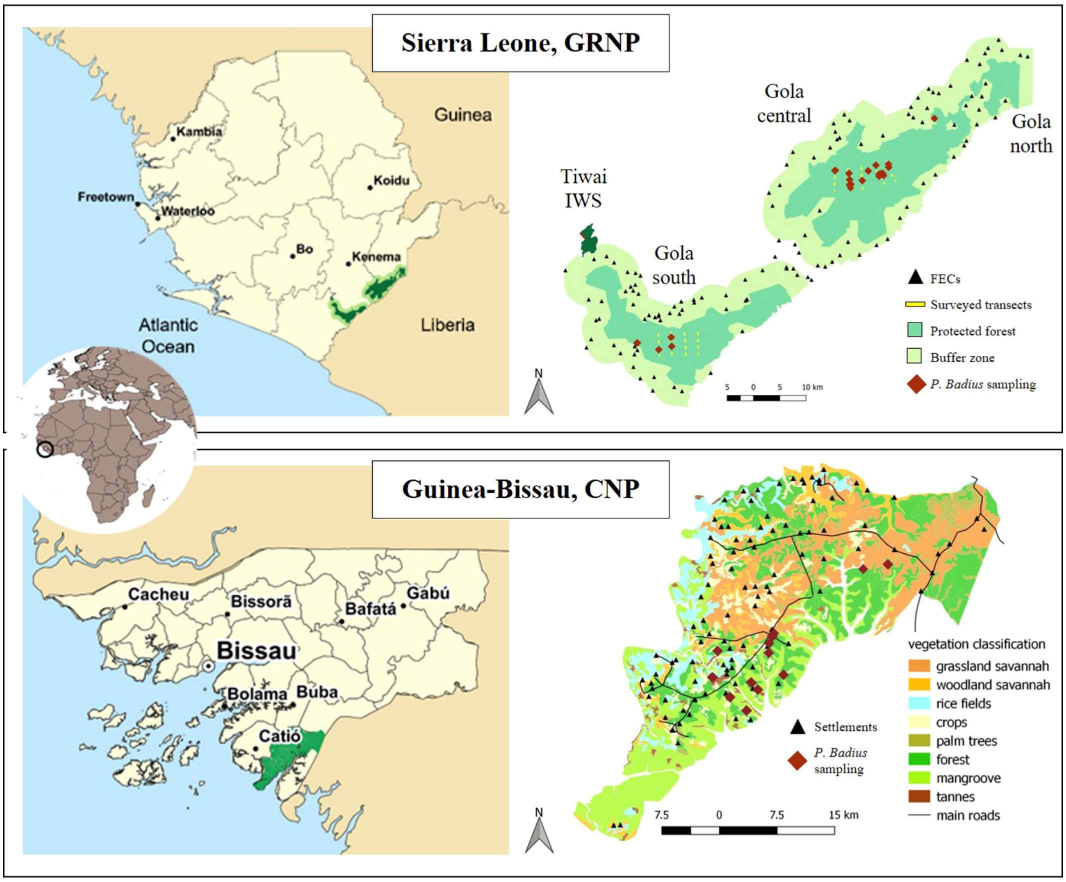

FIGURE 1
Maps indicating the locations of each PA in the countries, and where western red colobus non-invasive sampling took place (red diamonds). Gola Rainforest National Park (GRNP) in Sierra Leone is a protected forest composed of three forest blocks: Gola north, Gola central, and Gola south. The latter is where logging occurred more intensely across the PA. GRNP is surrounded by the community forest (buffer zone), where 122 villages (Forest Edge Communities – FECs) are located. In the southwest of the park, is the 12 km^2 Tiwai Island Wildlife Sanctuary, a community conservation initiative established in 1987. Cantanhez National Park (CNP) in Guinea-Bissau has a higher degree of forest fragmentation and different vegetation types, characteristic of the CNP. The map depicts the location of all 110 villages within the national park and also the main road that crosses the PA from north to south.

following historical logging exploitation and the use of the forest by militias and local communities during the civil war (1991–2002). There are no human settlements within the PA and anthropogenic activity is minimal, mainly due to heavy conservation patrol and the presence of researchers, although there are over one hundred villages with agricultural fields in the community forest (4 km wide area surrounding the protected forest). Cantanhez National Park (CNP) is a peninsula of roughly 1,000 km^2 of a mosaic of sub-humid forest, secondary forest, savanna, mangrove, human settlements and agricultural fields in the southwest of Guinea-Bissau. The PA is densely populated by communities of diverse cultural groups who exploit naturally occurring trees (e.g. the palm *Elaeis guineensis*) and cultivated species (e.g. *Anacaridum occidentale*). These cash crop plantations have contributed to a small increase in vegetation cover in the park since the 1950s (Catarino and Palminha, 2018). Although flora and fauna are diverse, threats to biodiversity include deforestation from slash and burn practices, bushmeat hunting, invasive species, climate change, and reduced law enforcement and protection (Hockings and Sousa, 2013; Catarino and Palminha, 2018).

2.2 Sample collection

Between April–June and November–December 2018, we surveyed high primate density areas in GRNP (identified previously in Klop et al., 2008; Ganas, 2009; Brncic et al., 2010; Barca et al., 2018), among the most pristine forests in Gola central and south. We used research line transects established by GRNP, sampling five transects in Gola south, eight in Gola central and one site in the community forest where chimpanzees (*Pan troglodytes verus*) were observed. Each transect (<4 km) was surveyed twice due to returning to camp on the same path. To maximise sampling, we opportunistically collected primate faecal samples whenever we detected individuals visually or acoustically. A total of 382 putative red colobus faecal samples were collected in the field. In 2019, we conducted fieldwork in CNP, Guinea-Bissau between March–April, and October–November. We visited the best-preserved forest fragments in CNP known to harbour the target species (Minhós, 2012) and, in the absence of established transects, we travelled through paths used by local people. We surveyed 15 forest patches and the forest around the base camp in Jemberém

(Figure 1). A total of 235 putative red colobus faecal samples were collected in CNP. Across both PAs, 617 primate faeces were sampled and preserved directly in HDPE plastic bottles (50 mL sterile screw top tubes) containing desiccating silica gel. This technique preserves samples unrefrigerated and allows DNA extraction from the host (primates) and all other organisms in its diet, including plants.

2.3 DNA extraction and metabarcoding amplification

Host and dietary DNA were extracted from ~200 mg of each faecal sample, using the QIAmp DNA stool kit (Qiagen, Manchester, UK), following manufacturer guidelines with slight modifications to reagent volumes, incubation and centrifugation periods. For each set of samples extracted, a positive and a negative control were added, with the latter used during DNA metabarcoding analysis. A total of 352 DNA samples barcoded taxonomically for western red colobus were selected for DNA metabarcoding. In addition, 60 DNA samples of *badius* previously collected in CNP during the 2009 dry season were added (Minhós, 2012).

Presence of plant DNA in 412 primate faecal extracts was confirmed with Polymerase Chain Reaction (PCR) amplification of the second internal transcriber spacer (ITS2) of nuclear ribosomal DNA using universal plant primers UniPlantF (5'-TGTGAATTGC ARRATYCMG-3') and UniPlantR (5'-CCCGHYTGAYYTGRGG-TCDC-3'), following Moorhouse-Gann et al., 2018. A unique combination of 10 bp molecular identifier (MID) tags was added to each sample for faeces identification in the post high-throughput-sequencing (HTS) step. PCRs of 25 µL reaction volumes containing final concentrations of 2.5× multiplex master mix and 2.5 µL of Q solution (Qiagen), 1.0 µM for each primer and ~ 60 ng of template DNA were performed. The PCR cycle initiated with a denaturation step of 95 °C for 10 minutes, followed by 40 cycles at 95 °C for 30 s, annealing temperature of 56 °C for 30 s, and 72 °C for 60 s, and a final extension of 10 min at 72 °C (Moorhouse-Gann et al., 2018). Each 96-well PCR plate included 80 primate samples, 12 negative controls, two blank controls and two positive controls. Negative controls were either extraction or initial PCR negatives treated as DNA samples and used to test primer contamination for each MID-tag. Blank samples (PCR mix and nuclease-free water) were placed in unused MID-tag combinations to identify tag-jumping. Positive controls were a mixture of plant DNA non-native to Africa used for amplification success and artefacts. Amplification of plant DNA was verified in 2% agarose gels and only samples that successfully amplified were selected to go through library preparation for 250-bp paired-end Illumina MiSeq HTS.

2.4 Library preparation and sequencing

All 374 (MID) tag PCR products were quantified (ng/µL) on a QIAxcel Advanced System (Qiagen) and negative controls were checked for PCR contamination. If contamination was detected, the PCR was repeated. Sample pooling for each 96-well PCR plate was based on equimolar concentrations among plant DNA samples, and the volume for negative and blank samples was the same as the average volume of plant DNA. Each pool of samples was cleaned using SPRIselect beads (Beckman Coulter, Brea, USA) in a ratio of 1:1.1 to retain fragments between 300 and 500 bp (ITS2 fragment size after (MID) tag PCR), and its concentration determined after clean-up using a Qubit dsDNA high-sensitivity assay kit (~61.7 ng/µL). Each sample pool was normalised to 100 ng of DNA for adaptor ligation under Illumina sequencing library preparation using a NEXTflex Rapid DNA-Seq Kit (Bio Scientific, Autin, USA) and AMPure XP Beads clean-up. A different Illumina index was assigned to each sample pool, and pools were sequenced for 250-bp paired-end reads using a Reagent Kit v2 on a Illumina MiSeq desktop sequencer (Illumina, San Diego, CA, USA). The sequencing and subsequent cleaning stages produced a dataset with 368 red colobus samples with good quality plant reads, five samples with zero plant reads, and one sample that showed some evidence of contamination. Six samples with no-results or contamination were excluded from the final dataset.

2.5 Bioinformatics and taxonomic identification

The bioinformatics pipeline followed Drake et al. (2022) with modifications following updated programs and improved methodology in the taxonomic assignment step. The pipeline was performed under LINUX and comprised programs and scripts written in BASH and PERL. Raw sequences were trimmed, aligned and checked for quality of reads using FastP v0.20 (Chen et al., 2018). Reads with q-score lower than 33 were discarded. Mothur v1.46.1 (Schloss et al., 2009) was used to assign reads to the respective sample IDs, according to the (MID) tag primer combinations, allowing for a minimum of one mismatch. Next, demultiplexing merged all reads from each sample into one fasta file. Usearch v11 was used with the Unoise3 command to denoise and remove chimeric sequences, and group identical sequences into zero radius operational taxonomic units (zOTUs). These were generated using a clustering identity threshold of 100% to avoid multiple species being grouped under the same OTU (conservative algorithm). At this stage, read abundance matrices (number of each zOTU reads per sample) were created along with a zOTU list, and further data clean up and filtering was performed with a combination of manual and Microsoft Excel processing. Reads originating from contamination, tag jumping and bleeding of over-represented taxa into other samples were removed using the combined maximum read count for blank, extraction negative and MID-tag PCR negative samples (Drake et al., 2022). A per zOTU threshold of 1% was further applied to eliminate low read counts. The value of the threshold was taken from a study that assessed contamination rates in complex field environments where samples are exposed to non-food DNA on the ground (Ando et al., 2018). After these cleaning steps, taxa were reduced by 24% but this more conservative approach was selected so plant diversity detected would not be inflated.

Taxon information for each taxonomic unit was obtained by comparison with sequences on the most up to date eukaryote nucleotide database from NCBI GenBank (2022). The BLASTn v2.12.0 (Altschul et al., 1990) was used in BLAST+ (Camacho et al., 2009) with a minimum percentage identity score of 96.02%, a value based on the mean value for the average genetic distances of sister species in angiosperms (3.98%, Qin et al., 2017). Additionally, the zOTUs retained were selected based on the plant species listed on both PAs botanical surveys (Klop et al., 2008; Catarino and Palminha, 2018) and presence in west Africa, or the African continent. In some cases, taxonomic identification could not be achieved for species, so genus or family identification was used. Fungal or bacterial sequences or other types of contamination (e.g. *Homo sapiens*, starch – *Solanum* spp. originating from the extraction kit spin columns) were not considered.

2.6 Dietary statistical analysis

A final dataset comprising 368 western red colobus samples (GRNP = 207; CNP: 2019 = 101, 2009 = 60) was transformed into presence/absence data, and frequency of occurrence (Fo%) was calculated for each zOTU. All statistical analyses were conducted in R Statistical software v4.1.3 (R Core Team, 2022).

Hill-diversity and sample coverage were estimated for each PA to assess dietary diversity and sampling efficiency of this study (Hill, 1973; Roswell et al., 2021). This method was preferred over sample size and effort-based standardisation, and asymptotic species-accumulation curves because they fail to account for the species-abundance distribution of the community sampled (Roswell et al., 2021; Tercel et al., 2022). Hill diversity is measured as the generalised mean species rarity and three exponents can be used to determine the sensitivity of the equation to rare species. All exponents were tested using the R package *iNEXT* (Hsieh et al., 2016): the most sensitive Hill-richness ($_l = 1$), Hill-Shannon ($_l = 0$) which responds to both high and low rare species, and the least sensitive Hill-Simpson ($_l = -1$).

To evaluate seasonal variation in dietary composition, a model-based approach in the *mvabund* R package (Wang et al., 2012) using simultaneous GLMs (generalised linear models; function 'ManyGLM'), a binomial error family and respective link function, and Monte Carlo resampling method were implemented. Data residuals were checked for normality for the modelled GLMs and Likelihood ratio tests (LRT), and resampled p-values are presented for the models selected. For visualisation purposes we used *Vegan* (Oksanen et al., 2019) and *ggplot2* (Wickham et al., 2016). The same approach was used to identify the effect of sex, time and habitat in the diet of western red colobus. Dietary variation was compared between 112 females and 42 males in the GRNP population (smaller dataset due to unsuccessful amplification of the sex marker for some samples), between CNP populations sampled in the same four forest patches in 2009 (N = 53) and 2019 (N = 14), and between areas of each PA with distinct differences in vegetation. In GRNP, the south forest block was intensively logged, leading to the presence of more secondary forest. The dataset is smaller (91 samples from Gola central, 31 samples from Gola south) and it represents the rainy season only, as no samples were obtained for red colobus during the dry season in Gola South. In CNP, the north of the park is mainly covered by savanna, and less forest and mangrove. However, due to the small sample size in this region, a similar spatial comparison was not possible.

Mean plant richness per sample was calculated for the diet of *badius* populations in each PA and compared using non-parametric Kruskal-Wallis tests to determine significant differences between PAs, females and males in GRNP, red colobus in Gola central and south, and by individuals sampled in 2009 and 2019. Levin's index of niche breadth (Levins, 1968) was estimated to compare the use of forest resources by the same groups of red colobus as above. We used the 'niche.width' function of the R package *spaa* (Zhang and Zhang, 2013) and standardised it with equation one from Razgour et al. (2011).

3 Results

3.1 Data filtering

The HTS generated approximately 12.39 million reads, reduced to 6,967,262 reads following filtering. An average of 7,147 DNA reads (± 3,593 SE) were obtained per sample and a total of 14,867 zOTUs compared with the NCBI GenBank reference database. Several zOTUs were discarded due to no or unsure taxa assignment (9.9%), taxa not native to or introduced in west Africa (1.1%), assigned to bacterial taxa (0.2%) and to fungi (3.4%). This last percentage is relatively high, possibly because the marker is also a universal barcode for fungi (Schoch et al., 2012) and some samples had developed fungi during the storage period. This study identified 1,699 dietary presence counts in 368 western red colobus samples, belonging to 97 plant taxa.

3.2 *Piliocolobus badius* diet

Western red colobus yielded 97 plant taxa (64 plant species and 33 genera) in the diet across the years and PAs, belonging to 40 families. An average of 4.48 plants (± SE 1.84) were detected in each sample with a minimum of one and a maximum of 11 taxa per sample. One fifth of plant taxa were detected in one single sample but it was still included in the analysis as this is a result obtained after cleaning the dataset for contamination. Overall, Hill-diversity estimates suggest that sampling conducted in both PAs was sufficient to cover a large majority of the dietary community (Figure 2, top graph). Less than 5% of the dietary taxa were not detected for each sample subset (dietary coverage ±95% CI: GRNP = 98.1 ± 0.9; CNP = 98.6 ± 0.9). The Hill-richness exponent ($_l = 1$) provided higher diversity estimates than the other two exponents (Hill-Shannon, $_l = 0$; Hill-Simpson, $_l = -1$), which reach an asymptotic result at the same number of detections (read counts). This shows that the dietary community of western red colobus comprises many plant taxa consumed infrequently, as exponent $_l = 1$ is more sensitive to rare species (Figure 2, bottom graph).

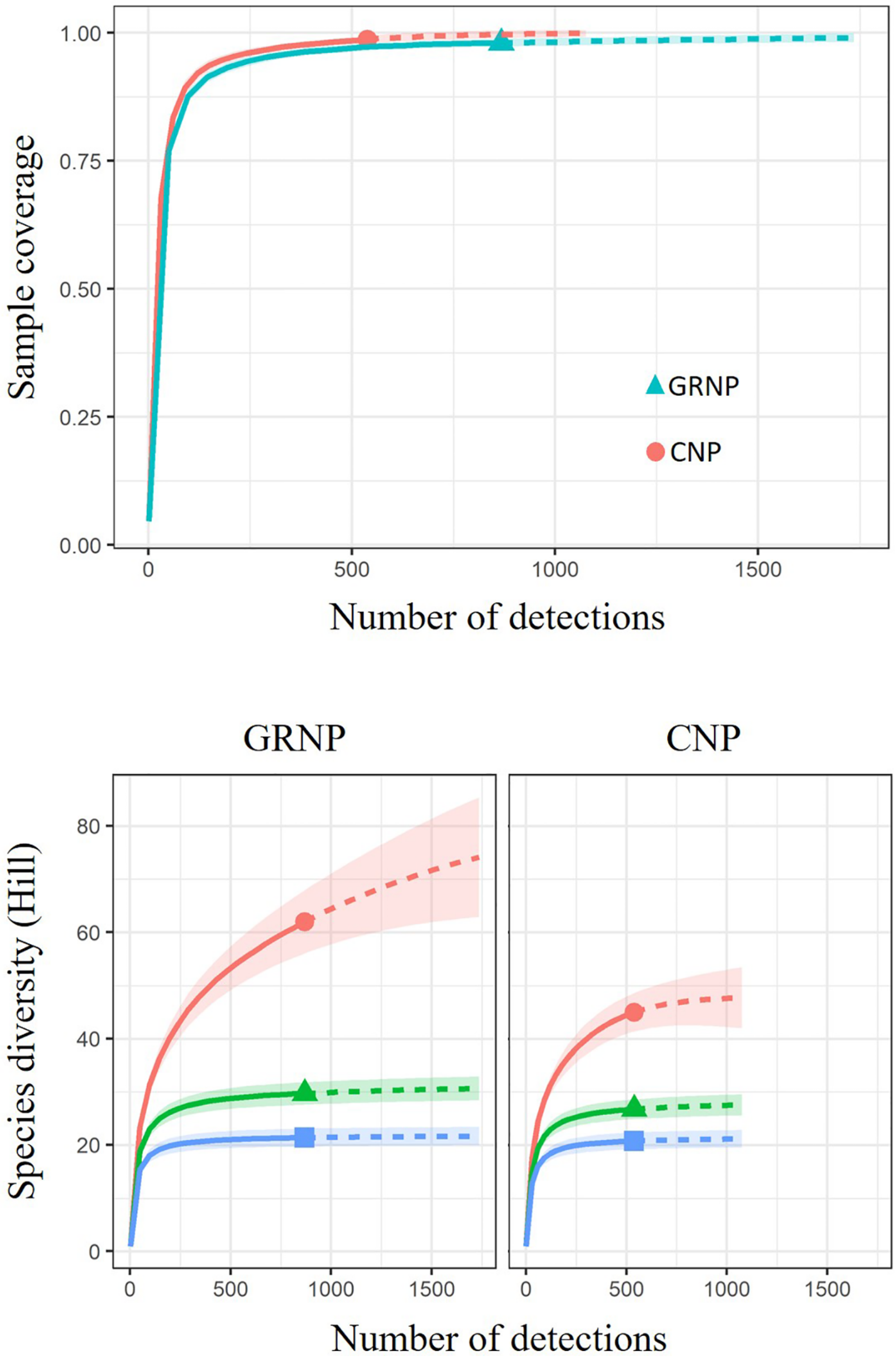

FIGURE 2
Plant species diversity and level of community coverage in the diet of western red colobus. The top graph demonstrates how much dietary community was possible to cover per number of detections for *badius* populations of GRNP (blue line and triangle) and CNP (red line and circle). These observations are extrapolated and shown by the dashed lines. On the bottom graphs, the percentage of plant taxa by number of dietary detections, generated with a DNA metabarcoding approach, is estimated in each protected area (GRNP and CNP). Results show three exponents with higher (1) to lower (–1) sensitivity to rarely consumed food items: Hill-richness (*l* = 1), red line with circle; Hill-Shannon (*l* = 0), green line with triangle; Hill-Simpson (*l* = –1), blue line with square. Solid lines are the observed diversity, which are further extrapolated (dashed lines). Shading around the line corresponds to 95% confidence intervals.

All plants detected in the diet of western red colobus were present in the botanical surveys conducted in each PA or have been recorded in the countries where sampling took place. More than half of these species were recorded as food items in previous red colobus research (Supplementary Tables S3–S5; Table 1) and represent plants with the highest frequency of occurrence in this study. The plants detected in the diet of the GRNP population belong mostly to the Fabaceae family (18.4% – one of the most

TABLE 1 Information on the present and previous dietary studies on red colobus (*Pilicolobus* spp.) across Africa.

Piliocolobus (sub) species	Study period	Study site, PA country	Study period (years)	Nb. plant species consumed	Top plants	Source
P. badius badius	1999	Tiwai IWS, Sierra Leone	1	47	◆ *Funtumia africana* ◆ *Amphimas pterocarpioides* ◆ *Detarium senegalense*	(Davies et al., 1999)
	2010–2014	Taï Forest, Côte d'Ivoire	< 2	32	◆ *Caloncoba brevipes* ◆ *Strephonema pseudocola*	(McGraw et al., 2016)
	2017	Taï Forest, Côte d'Ivoire	0.6	34	◆ *Scytopetalum tieghemii* ◆ *Lophira alata*	(Wilkins, 2017)
	2018	Gola RNP, Sierra Leone	0.5	62	◆ *Lophira alata*	Present study
P. badius temminckii	1977, 1978	Abuko, The Gambia	1	39	◆ NA	(Gatinot, 1977; Gatinot, 1978)
	1991	Abuko, The Gambia	1	89	◆ NA	(Starin, 1991)
	2019	Cantanhez NP, Guinea-Bissau	0.3	45	◆ *Treculia africana*	Present study
	2009	Cantanhez NP, Guinea-Bissau	1	36	◆ *Parinari excelsa*	Present study
P. kirkii	1991, 1993	Jozani, Tanzania	1	62-63	◆ NA	(Mturi, 1991; Mturi, 1993)
P. preussi	2001	Korup, Cameroon	1.3	17	◆ NA	(Usongo and Amubode, 2001)
P. rufomitratus	1994–1999, 2006–2007	Kibale, Uganda	1.7	31	◆ *Celtis durandii* ◆ *Celtis africana*	(Ryan et al., 2013)
	1981	Tana River, Tanzania	1.3	22	◆ *Ficus sycomorus* ◆ *Sorindeia excelsa* ◆ *Strombosia scheffleri*	(Marsh, 1981)
P. tephrosceles	1970–1972	Kibale, Uganda	1.6	46	◆ *Celtis africana*	(Struhsaker and Oates, 1975)
	1972–1987	Kibale, Uganda	9.9	85	◆ *Celtis africana*	(Struhsaker, 2010)
	1976–1983	Kibale, Uganda	3.8	70	◆ *Morus lacteal* ◆ *Newtonia buchananii*	(Struhsaker, 2010)
	1975	Gombe, Tanzania	0.9	>58	◆ *Celtis durandii* ◆ *Parinari excelsa* ◆ *Stombosia scheffleri*	(Clutton-Brock, 1975)
	2011	Mbuzi, Tanzania	0.2	36	◆ *Parinari excelsa*	(Kibaja, 2014)
P. tholloni	1994	Botsima, Zaire	1	84	◆ NA	(Maisels et al., 1994)

Nb. plant species consumed, only those for which identification was possible; Top plants, the ones primates spend more time feeding on or that were more frequently detected in faeces. Previous studies used traditional feeding ecology methods, such as direct observations and morphological examination of plant parts in the faecal matter, while the present study used a DNA metabarcoding approach.
NA, information not available.

common plant families in the park), Combretaceae (12.7%), Rubiaceae (9.6%) and Chrysobalanaceae (9.2%). These plants are mainly trees and shrubs, with vines and climbers being detected in fewer samples. A total of 62 plant taxa were identified in the diet of the GRNP population, and the top species consumed were *Lophira alata*, *Anthonota macrophylla*, *Combretum* spp. and *Maranthes aubrevillei* (Supplementary Table S3). We identified 45 plant taxa from 24 families in the diet of the CNP population sampled in 2019. Fabaceae, Moraceae and Rubiaceae contributed to nearly 50% of the primate diet. *Treculia africana* was detected in more than half of the samples, and four other species were present in more than 35–40% faecal samples (Supplementary Table S4). Trees and shrubs were identified as the most important in the diet of this population.

3.3 Dietary variation

3.3.1 Seasonal variation

The top 20 plant taxa were all present in GRNP samples collected in the dry and rainy seasons, except *Nauclea* spp. which was only detected in samples collected during the rainy season. Fewer plant taxa were detected in the dry than in the rainy season (plant taxa: dry = 35, rainy = 54), but mean plant richness per sample was similar between seasons (dry = 4.23, rainy = 4.16; W = 5299.5, *p*-value > 0.05). However, seasonal dietary composition varied significantly (LRT = 328.1, *p*-value = 0.001; Figure 3). Seven plants contributed to this variation (*p*-value < 0.05) with the most significant being *Cryptosepalum tetraphyllum* only consumed in the dry season, and *Nauclea* spp. detected only in the rainy season.

The most frequently detected plant taxa for the red colobus of CNP were all native to Guinea-Bissau, with *Treculia africana* being detected in more than 50% of samples. Most plants were detected in both seasons, with a few only present in the rainy (e.g. *Uncaria africana*) or dry season (e.g. *Ceiba pentandra*). Despite the total number of plants detected in samples from the 2019 dry season being higher (plant taxa: dry = 37, rainy = 28), the mean plant richness per sample was significantly lower than in the rainy season (dry = 4.69, rainy = 6.64; W = 480.5, *p*-value < 0.001). The MGLM model revealed that dietary composition in the dry and rainy seasons was significantly different (LRT = 398.6, *p*-value = 0.001, in Figure 3), and three of the twelve plant species that had a significant effect on seasonal variation (*p*-value < 0.02) were consumed in the dry season (*Cryptosepalum tetraphyllum*) or in the rainy season (*Nauclea* spp. and *Daniellia ogea*).

3.3.2 Biological variation

Differences in the number of plants (females = 4.06, males = 4.4; W = 1966, *p*-value > 0.05) or the type of plants ingested (LRT = 5.66, *p*-value = 0.134) by female and male red colobus of the GRNP population were not significant. Dietary niche for females and males of red colobus from GRNP was equal (Levin's niche = 0.11). The overlap of the items detected in the diets of the two groups is clearly observed in the NMDS plot (Figure 4A).

3.3.3 Ecological variation

We detected significant differences in the mean number of plant taxa in red colobus from Gola central and Gola south blocks during the rainy season (Gola central = 4.5, Gola south = 3.0; W = 1849.5, *p*-value < 0.001), and in the variation of the dietary composition (LRT = 8.46, *p*-value = 0.001; Figure 4B). Nine plants contributed significantly to this variation (p-value < 0.05), with three of the most significant taxa being detected in Gola central samples only (*Anthonotha* spp., *Maranthes aubrevillei* and *Pentadesma butyracea*) and two mainly in Gola south (*Terminalia* spp. and *Trichilia monadelpha*). Niche width was wider for the red colobus groups in Gola central (0.10) than those in Gola south (0.04).

3.3.4 Temporal variation

The CNP red colobus population was sampled with a ten-year gap, in the dry season of 2009, and in the dry and rainy seasons of 2019. Additionally, only four of the forest patches were sampled at both time periods so, for comparison purposes, we only analysed samples from the dry season and from the following forests: Caghode, Cambeque, Jemberém and Madina. Plant species diversity was higher for the population sampled ten years ago but so was sample size (2009 = 54 samples, 32 taxa; 2019 = 14 samples, 22 taxa). Nonetheless, the mean number of plants in each sample was significantly different between years (2009 = 3.80, 2019 = 5.0; W = 240.5, p-value = 0.042) and Levin's niche was wider in 2009 (2009 = 0.09, 2019 = 0.06). Moreover, even though dietary

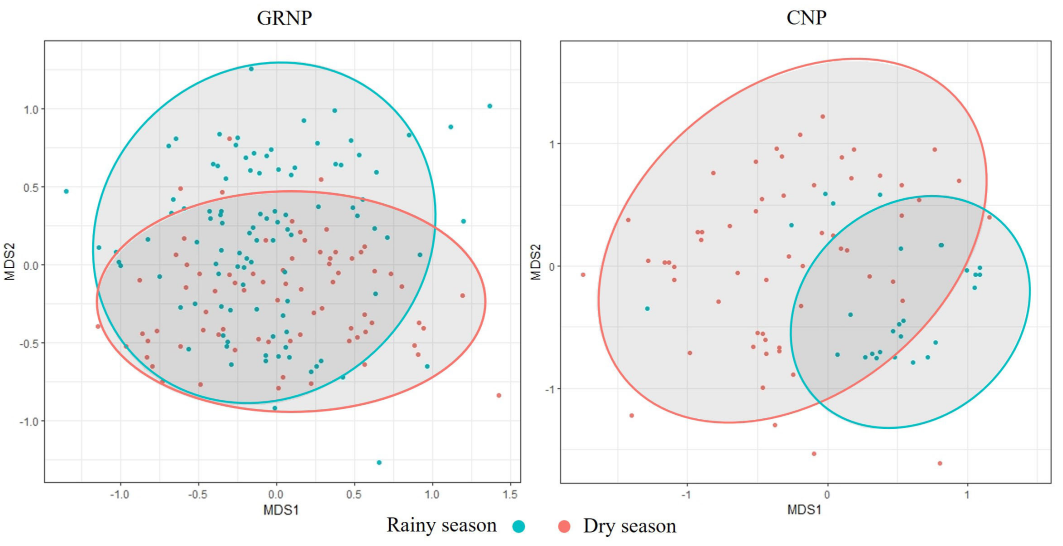

FIGURE 3
Seasonal dietary variation of the GRNP (N = 207) and CNP (N = 101) populations, represented by pairwise biplots from non-metric multidimensional scaling (NMDS) analysis. The diet of *badius* varied significantly between the dry season (red dots and ellipse) and the rainy season (blue dots and ellipse).

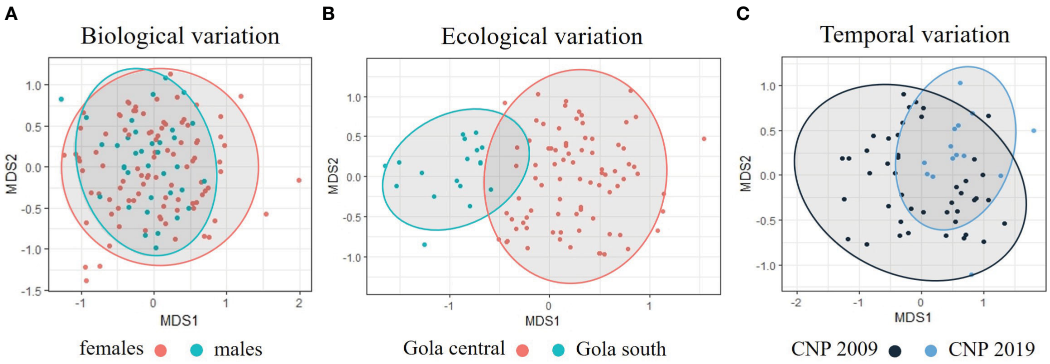

FIGURE 4
Biological, ecological, and temporal variation in the dietary composition of western red colobus is illustrated in three pairwise biplots from non-metric multidimensional scaling (NMDS) analysis. Panel **(A)** shows a non-significant variation in dietary composition of female (red circles and ellipses) and male red colobus (blue circles and ellipse). The NMDS plot **(B)** illustrates a significant variation in the food items consumed during the rainy season by *badius* individuals living in Gola central (red circles and ellipses) and Gola south (a more degraded forest in GRNP; blue circles and ellipse). The plot on the right **(C)** represents the significant variation in dietary composition of red colobus individuals sampled in 2009 (dark blue circles and ellipse) and in 2019 (light blue circles and ellipse).

composition between time periods showed significant variation (LRT = 7.2, p-value = 0.005), the diet of individuals highly overlaps across time (Figure 4C), with only two plant species significantly contributing to the variation (*Ceiba pentandra* and *Treculia africana*) which were present in both time periods, but at a much lower frequency in 2009 (~14%; in 2019, 64%).

3.4 Dietary flexibility under different ecological conditions

The diet of the GRNP and CNP populations varied in the raw count of plant taxa and mean number of plants detected per sample (Table 2). Total plant richness was higher in GRNP than in CNP,

TABLE 2 Plant dietary richness of western red colobus populations of GRNP and CNP, compared across protected areas, habitat types, and time periods.

	PAs		Less vs more degraded forest				Degraded forests		Time periods	
	GRNP	CNP	GC	CNP	GC	GS	GS	CNP	CNP 2009	CNP 2019
Seasons	Dry & Rainy		Dry & Rainy		Rainy		Rainy		Dry	
Sample size	**207**	**101**	**182**	**101**	–	–	–	–	–	–
dry season	90	68	91	68	–	–	–	–	54	14
rainy season	117	33	91	33	91	27	27	33	–	–
Total nb. plant taxa	**62**	**45**	**59**	**45**	–	–	–	–	–	–
dry season	35	37	36	37	–	–	–	–	32	22
rainy season	54	28	51	28	51	18	18	28	–	–
Mean nb. plant taxa per sample	**4.19**	**5.33**	**4.36**	**5.33**	–	–	–	–	–	–
dry season	4.23	4.69	4.22	4.69	–	–	–	–	3.80	5.00
rainy season	4.16	6.64	4.51	6.64	4.51	3.00	3.00	6.64	–	–
% crops in diet	**3.23**	**11.11**	**3.38**	**11.11**	–	–	–	–	–	–
dry season	5.71	10.81	5.55	10.81	–	–	–	–	3.13	9.09
rainy season	1.85	10.71	3.92	10.71	3.92	0.00	0.00	10.71	–	–
Levin's niche breadth *	**0.120**	**0.116**	**0.113**	**0.116**	**0.100**	**0.035**	**0.035**	**0.078**	**0.087**	**0.057**

GRNP, Gola Rainforest National Park; CNP, Cantanhez National Park; GC, Gola central; GS, Gola south; CNP 2019 and 2009 sampled in four common forests. % Crops: the number of plants detected in red colobus diet that is a cultivated or introduced item. * Levin's niche breadth adjusted using Razgour et al. (2011) equation.

Total number of plants and mean number of plant taxa per sample detected under the DNA metabarcoding approach are enumerated in the table yearly and per season. The percentage of *Piliocolobus badius* diet that consists of cultivated food items is shown, along with the niche width (Levin's niche breadth) for each dataset analysed.

despite botanical surveys providing similar numbers of recorded plants (899 species in GRNP, 863 species in CNP). However, mean plant richness per sample detected in red colobus diet from GRNP was significantly lower than in CNP ($t = -3.37$, $df = 309.63$, $p\text{-value} < 0.001$). Niche breadth was also narrower for the CNP (0.116) than for the GRNP population (0.120). As Gola south has been intensively used for logging and the vegetation is expected to contain a certain degree of secondary forest resembling a more degraded habitat, we tested the differences in the mean plant richness per sample against CNP, a degraded forest, and between CNP and Gola central only, as this most closely resembles a pristine forest within our dataset. Levin's niche standardised with Razgour et al. (2011) equation was also calculated. We detected significantly fewer plants in the diet of red colobus sampled in Gola south during the rainy season, than in those from CNP during the same season (Gola south = 3.0, CNP = 6.64; $W = 43$, $p\text{-value} < 0.001$), and a narrower niche (Gola south = 0.04, CNP = 0.08). A similar pattern was detected between the continuous and well protected forest of Gola central and the altered landscape of CNP across both seasons (Gola central = 4.36, CNP = 5.33; $W = 6547$, $p\text{-value} < 0.001$), although niche width was similar (Levin's niche for GRNP = 0.11 and CNP = 0.12).

3.4.1 Consumption of cultivated plant species

Just over 7% of western red colobus diet, across study sites and years, comprises crops (defined here as native or introduced plant species cultivated in farming grounds outside or within the PAs, or naturally growing in the forest and exploited by local human communities). One introduced (*Enterolobium* spp.) and two native plants exploited by humans in Sierra Leone (*Cola* spp. and *Coffea* spp.) were detected for the GRNP population, but they were rarely present across samples ($F_o < 2.5\%$; Supplementary Table S3). Despite being native, Kola trees are sometimes grown as crops by local villagers. However, as in this PA most red colobus groups occur within the protected forest and so did the sampling, *Cola* spp. will not be considered a crop. Hence, crops *Enterolobium* spp. and *Coffea* spp. accounted for 3.2% of *badius* diet in GRNP. Both items were eaten during the dry and rainy season, but *Coffea* spp. had a higher frequency of consumption in the dry season, when the unripe fruit is available. The percentage of crops identified for samples in Gola central during the rainy season was 3.9, while absent in samples from Gola south. A higher number of crops was identified in the dietary composition of the red colobus population of CNP (11%). However, all items had low frequencies of occurrence compared to the wild plant taxa consumed: mango (8.9%), coffee (4%), *Solanum* spp. (2%), cashew (1%) and *Cucumis* spp. (1%) (Supplementary Table S4). In the 2009 dataset, we detected one single crop (*Mangifera indica*) with a F_o of 33.96% in the diet of the red colobus group from Jemberém forest, the closest group to a human settlement (Supplementary Table S5). In 2019, crops were present three times more in the diet of *badius* than in 2009, and with higher frequencies of occurrence (*M. indica* = 64.29%, *Solanum* spp. = 7.14%). Again, the group which consumed more crops was the one sampled in the neighbouring forest of Jemberém. However, in the more recent sampling period, another *badius* group occupying a forest close to the village of Madina also consumed cultivated items.

4 Discussion

4.1 Western red colobus diet

This study is the first application of DNA metabarcoding sequencing to investigate the diet of western red colobus species in west Africa. The method proved successful when using non-invasive samples, yielding 97 plant taxa (62 for the GRNP population and 45 in CNP) in the diet of *Piliocolobus badius*. Four to five plant taxa were most frequently detected in the diet of each *badius* population, suggesting a degree of dietary specialism and the importance of those plants for the survival of these threatened primates. Red colobus preferentially feed on the largest and most common plant species in their habitat (Oates, 1994), here observed in the GRNP population (e.g. *Lophira alata*, *Maranthes aubrevillei*, Supplementary Table S3) over other taxa. *Lophira alata* was also identified as an important food item for the red colobus population of Taï, Côte d'Ivoire (Wilkins, 2017). It was not possible to infer a similar correlation for the CNP population as abundance data for plant species is not yet available for this PA. However, should our results support the theory, we could suggest that *Treculia africana*, *Parinari excelsa* and *Malacantha alnifolia* could be some of the largest and more common trees in CNP, as they had the highest frequencies in *badius* diet (Supplementary Tables S4, S5). As for *badius* of Taï and in Tiwai and for *rufomitratus* in Kibale, Uganda (Davies et al., 1999; Ryan et al., 2013; Wilkins, 2017), figs from *Ficus* spp. and fruits of *Parinari excelsa* trees were important food items for the CNP population (F_o >30%). These two plant taxa are present in most habitats of the CNP, suggesting that red colobus inhabiting more degraded forest patches still have access to important foods.

Although DNA metabarcoding does not provide quantitative data for the items consumed, the frequency of occurrence demonstrates the most commonly present plant taxa in the diet of red colobus. In this study, trees and shrubs were the most detected plant types, reflecting arboreal behaviour of *Piliocolobus*. The present study detected a higher dietary richness for *badius* than previous studies employing traditional methods to study the feeding ecology of red colobus species across Africa for longer periods of time (min. = 17, max. = 89 plant species; Table 1). This was expected, as DNA metabarcoding is a more robust technique featuring higher taxonomic resolution to detect rarer food items consumed or more easily digestible foods (Pompanon et al., 2012; Ando et al., 2013; Sousa et al., 2019). The efficiency of the method is further supported by the high proportion of plant taxa identified that did not occur frequently in the diet of the sampled individuals, and that have not been reported in previous red colobus dietary studies.

4.2 Variation in diet

Females and males did not have significantly different diets (Figure 4A), despite assumptions that overall energy costs are greater for females than males associated with gestation and lactation (Key and Ross, 1999). Dietary variation between seasons, habitats and time periods was significant. Annual fluctuation in the diet of western red colobus was observed in both PAs (Figure 3), but results do not follow a specific pattern. Although the lack of phenology data during the study period does not permit a direct correlation with young leaves, seed and fruit availability, previous regional studies indicate that these plant parts are more commonly produced in the dry season (Munro et al., 2013; Bessa, 2014; Hockings et al., 2020). Overall, the GRNP population demonstrated a much higher consumption of different plant taxa during the rainy season (when preferred food is less available), while an opposite trend was observed for the CNP population (Table 2). These differences may reflect food availability in each habitat and food preferences by the primate groups within each population. Several years of data on the *b. tephrosceles* of Kibale forests (Uganda) suggest that significant inter-annual variation in dietary composition reflects the complex diversity of the habitat (Struhsaker, 2010). At the time of the study, Kibale was a relatively large old-growth rainforest, a type of habitat preferred by red colobus. However, only a few plant species accounted for the majority of the diet, reinforcing this species as a specialist consumer (Struhsaker, 2010). One limitation of DNA metabarcoding is the fact that food items cannot be quantified. Hence, the lower mean plant richness per sample observed in GRNP during the rainy season (Table 2) may indicate that red colobus consume higher quantities of few preferred foods to meet the daily nutritional requirements, but because individuals may have to cover a wider range of the PA during food scarcity and as a response to intra-group competition, it contributes to an increase in the total number of plant taxa consumed by the population overall. We cannot exclude the fact that competition for food with other sympatric primates with similar dietary requirements (e.g. *Colobus polykomos*, *Chlorocebus aethiops sabaeus*) may also influence the patterns we found. In this study, the top four trees and shrubs in the GRNP red colobus diet (Supplementary Table S3) can produce leaves mostly year-round, with simultaneous periods of flower and fruit production (Arbonnier, 2002), providing food even during low preferred food availability.

In CNP, more overall plant taxa were detected in the dry season but the mean plant richness per sample was significantly higher in the rainy season (Table 2). This contrasts with our inference for GRNP and may represent restricted food access in a more degraded habitat. As preferred food is less abundant in the rainy season, the CNP population, with a smaller area of forest to explore and likely less diverse plant species, reduced its plant taxa intake overall but each individual had to feed on more plants to meet its dietary requisites. Protein-to-fibre ratio of food items may determine leaf choice in herbivores, and hence limit colobine population size (Milton, 1979), while large groups have higher group feeding competition and require more energy for travelling in search of clumped food (Wrangham et al., 1993; Chapman, 2000). Therefore, as a response to low preferred food availability (with lower protein-to-fibre ratio), red colobus in CNP may have to cover different parts of the forests in their daily travel distance, increasing the number of plant taxa in the overall diet of the population. The most heavily consumed plant by the CNP population, particularly in the rainy season, was *Treculia africana* (Supplementary Table S4), which appears to provide food annually as the flowering period is from October until February, and its large fruits, containing many seeds, can be present all year-round depending on region and environmental conditions (USDA, 2015).

Spatial differences detected in the diet of GRNP red colobus during the rainy season showed each individual from Gola central feeding, on average, on more plant taxa than those from Gola south forest block, having a wider niche, and varying significantly in the plants consumed (Figure 4B). Variation in the vegetation cover, where Gola south is more likely covered by a higher area of secondary forest due to intense forest logging, could influence the type of preferred food availability, impacting directly on the dietary choices of red colobus. Indeed, two of the plants that contributed most to the dietary variation and were mostly consumed by the group in Gola south, can be used as timber (*Terminalia* spp.) or are a type of understorey plant of rainforest common in secondary growth areas (*Trichillia monodelpha*).

In a temporal analysis performed on the diet of *badius* in Taï forest (Côte d'Ivoire), where 20 years of vegetation transformation resulting from changes in the rainfall, fragmentation, and increased logging have taken place, there were clear reductions in dietary diversity and number of species consumed over time (Wilkins, 2017). This was also observed in the CNP population, but could be due to the small sample size in 2019 as the mean plant richness per sample was higher than in 2009. However, extant individuals have a narrower dietary niche and more frequently consume items from some of the largest trees in the park. The variation observed in the diet of red colobus from CNP across time requires further investigation, including temporal phenological surveys to elucidate whether changes are related to actual alterations in the vegetation or simply intra-specific food choices.

4.3 Dietary flexibility

Despite niche width being similar in both PAs, the population of GRNP fed on almost 20 more plant taxa than the CNP population. Hill-diversity indices indicate that this is a real difference and not an artefact of the different sample size (Figure 2). Nonetheless, the mean plant richness per sample was considerably higher for the CNP population. These results were similar to trends inferred in the comparison between Gola central (the most continuous and pristine forest) and CNP (degraded forest) populations, as well as for red colobus groups sampled at two time periods in CNP. It may be that in the degraded forests of CNP, particularly when preferred food is scarce, red colobus must feed on more plant species to meet dietary requirements, probably relying on many poorer quality foods. Contrastingly, *badius* inhabiting the well preserved, larger and more connected forest of GRNP can likely meet daily dietary requirements relying only on preferred plant species, which are available even during the most challenging season. However, spatial analysis in GRNP between less and more degraded forests (Gola central and Gola south, respectively), and the comparison between two more degraded habitats (Gola south and CNP), reflect dietary differences that cannot be directly associated with red colobus habitat (Table 2). The variation in the dietary patterns illustrated by this study pose a challenge for predicting western red colobus adaptation to rapid anthropogenic changes in vegetation, with unpredictable consequences to this endangered primate socio-ecology, namely group size and social structure, spatial distribution, daily travel or dispersal dynamics, and consequently long-term persistence. Another study of the impact of modified landscapes on the dietary flexibility of female red colobus in Kibale, Uganda, identified behavioural flexibility in the group living in the logged forest in comparison to the old-growth areas (Milich et al., 2014). Females from the logged areas fed on fewer resources from a greater number of plant species, enabling similar population densities to female groups in the old-growth areas.

Cultivated food items were more prevalent in the diet at both time points in CNP than in the GRNP population (Supplementary Tables S3–S5; Table 2). The inclusion of cultivated items in the diet of a highly forest-dependent primate is probably a response to living in a more degraded habitat and nearer cultivated fields, which provide access to more energetic food items. This behaviour has been observed in other populations of red colobus that could not meet the dietary requirements from preferred wild food due to forest degradation (Galat-Luong and Galat, 2005; Kibaja, 2014). The crops detected in the diet of red colobus in CNP are present near settlements, in gardens or in monoculture orchards. There are mango trees in the dense forest, but in general we demonstrate that *badius* is foraging on grounds that are commonly used by humans. *Coffea* spp. was consumed by red colobus in GRNP in both seasons, as was *Enterolobium* spp. Coffee trees are cultivated in orchards that are managed under an agroforestry system. As most coffee species are intolerant to direct sunlight and benefit from a soil enriched by the fallen leaves of high canopy trees (Alemu, 2015), farmers in Gola region plant coffee trees under tall trees (information provided by conversations with farmers during fieldwork and direct observations). In South America, farmers use *Enterolobium* spp. as a shading tree in coffee plantations, and some species of this taxa have been introduced in Sierra Leone, likely explaining our results. As we expected, the diet of red colobus from CNP included more human-cultivated foods, probably due to lower availability of forest, wild preferred foods, and the closer proximity with humans and therefore access to crops. This pattern is reinforced by the spatial distribution of faecal samples. In CNP samples were collected relatively close to human settlements, whereas in GRNP most samples were collected deep in the forest, distant from the villages and crops. Our results show that the different PA landscape and management strategies have a direct impact on the spatial distribution and habitat use by western red colobus, and consequently on the diet composition of this specialist primate.

4.4 Contribution to primate conservation

Habitat degradation due to vegetation loss, fragmentation and transformation to farmland is a major threat to red colobus population sustainability (Struhsaker, 2010; Linder et al., 2021). One solution to minimise biodiversity loss is to implement new and/or improve management of existing PAs. However, not all areas are suitable habitat for primates (e.g. sand dune vegetation, high altitude forests) (Estrada, 2006) and, although important for wildlife and ecosystem conservation, many do not offer the best conditions for primate populations to thrive (Chape et al., 2005). Many are poorly managed, understaffed or simply exist on paper, and are commonly small vegetation islands surrounded by altered landscape (DeFries et al., 2005; UNEP-WCMC, & IUCN, 2022). We suggest that the large and well preserved forest of GRNP may provide sufficient natural resources for western red colobus to maintain dietary requirements, but some evidence of dietary flexibility to habitats where humans are present is emerging. The fact that in the more disturbed forests of CNP, red colobus include more crops in its diet and, during the seasons of lower food availability, have to rely on more plant species to meet the dietary requirements show some level of dietary flexibility. This is also the case with other primates (e.g. *Pan troglodytes*, *Macaca* spp., *Cercopithecus* spp.; Hill, 2018). It is therefore essential to better understand how primates use agroforest areas, and plan, along with local communities, the most sustainable way to manage the landscape in order to improve non-human primate persistence in anthropogenic protected areas and local livelihoods. Work is already underway in GRNP, where cocoa beans from plantations with increased biodiversity are preferred to those that exclude animals that feed on this crop. This strategy could serve as a precursor to exploring the growth of other crops along with endemic species. In CNP, the complex and dynamic use of the landscape may have a significant impact on red colobus ecology as its flexibility to a disturbed environment is clearly visible from our results. Despite some dietary flexibility which currently allows the species to cope with a decrease in the forest habitat that is being converted into monocultures, reduced wild food resources may push red colobus individuals to live in smaller forest fragments with scarcer natural foods, and consequently rely more on human cultivated foods. Moreover, red colobus are a highly vulnerable and targeted primate for bushmeat hunting (Minhós et al., 2013), implying that a closer proximity to humans in search of food sources increases exposure to hunters and threatens survival. Overall, our results show that large and preserved forests are not only important to provide good quality food to maintain sustainable red colobus populations, but also ensure that these primates maintain a safer distance from neighbouring human communities.

5 Conclusion

Anthropogenic pressure will continue to affect natural habitats and weakly protected areas, and thus, well preserved forests like GRNP may play a crucial role in the socio-ecological stability of threatened non-human primate populations. Differences in red colobus diet, such as those detected within and between PAs in this study, could be explained by the nutritious value of each food item, plant species distribution and abundance across the landscapes, and consequently, seasonal food availability; but it could also reflect the dietary flexibility of this specialist primate species to the habitat. Identifying the cause of dietary diversity and variation proved difficult in this short-term research mostly due to the complex species socio-ecology and variations in natural resource availability. Therefore, it is important to use integrative approaches to understand how primates respond to habitat transformations in space and time, to provide and implement sustainable and achievable conservation strategies within and outside PAs. The identification of important plants in species diets is a key factor to consider for conservation management, including future reforestation campaigns. Strategic plant species and locations must be well defined for the sustainability of projects, including plant growth success and feasibility of habitat use by red colobus and other species, and its interplay with local livelihoods.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Files. Further inquiries can be directed to the corresponding author.

Author contributions

IAP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Visualization, Writing – original draft, Writing – review & editing. FB: Data curation, Methodology, Writing – review & editing, Investigation, Project administration. NS: Investigation, Writing – review & editing. MSo: Investigation, Writing – review & editing. MC: Investigation, Writing – review & editing. ITC: Investigation, Writing – review & editing. CR: Investigation, Writing – review & editing. BB: Project administration, Resources, Writing – review & editing. BST: Project administration, Resources, Writing – review & editing. MSw: Resources, Writing – review & editing. ARB: Project administration, Resources, Writing – review & editing. QQ: Project administration, Writing – review & editing. MJFDS: Investigation, Writing – review & editing, Funding acquisition. AFM: Resources, Writing – review & editing, Supervision. MWB: Project administration, Resources, Supervision, Conceptualization, Methodology, Writing – original draft. TM: Funding acquisition, Investigation, Writing – review & editing, Conceptualization, Methodology, Project administration, Resources, Supervision, Writing – original draft, Formal analysis, Visualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1280277/full#supplementary-material

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Wild ungulates and shrub control interact to restore herbaceous vegetation in shrub-encroached mesic grassland of South Africa

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Shrub encroachment threatens grassland ecosystem services including herbaceous plant diversity, productivity, and overall grazing capacity. Hence, various shrub control methods including mechanical removal and herbicides are applied to restore herbaceous vegetation. However, the knowledge regarding the outcomes of integrated shrub management on herbaceous vegetation is limited. We investigated herbaceous vegetation responses after 7 years following the integration of shrub control and herbivory at Telperion Nature Reserve, Mpumalanga Province, South Africa. In a split-plot experiment using four enclosures and non-enclosures as main plots, we randomly assigned each of the following treatments in four 4 × 4-m subplots in each main plot: 1) foliar metsulfuron-methyl herbicide, 2) 50% mechanical shrub removal, 3) 100% removal, and 4) no removal (untreated controls). A one-off *Seriphium plumosum* removal and the application of species-specific herbicide were conducted in 2015. Shrub control by herbivory interaction was significant ($p < 0.05$) for herbaceous canopy cover, basal cover, density, and species richness. The effects of herbivory were significant ($p < 0.05$) in the 50% removal treatment, increasing herbaceous plant diversity, density, and richness to the same level as 100% removal and herbicide treatments. In enclosures, however, the 50% shrub removal treatment attained relatively low herbaceous plant cover, density, species diversity, and richness compared to the herbicide treatment. Overall, this study revealed that herbivory and shrub control interact to facilitate herbaceous vegetation restoration, with 50% shrub removal by herbivory combination showing potential for management of *S. plumosum*-encroached grasslands.

KEYWORDS

enclosures, grassland ecosystem services, herbicide, herbivory, mechanical shrub removal, *Seriphium plumosum*

1 Introduction

Shrub encroachment defined as the increase in shrub cover, density, and biomass disrupts ecosystem processes and services and changes the structure and functioning of grasslands (Zhou et al., 2019; Mochi et al., 2022; Wieczorkowski and Lehmann, 2022). This phenomenon is ascribed to complex interactions of overgrazing and inappropriate fire regimes together with global drivers including elevated atmospheric CO_2 and variable rainfall regimes (Stevens et al., 2016). Overgrazing reduces herbaceous cover, abundance, and biomass, giving shrubs a competitive advantage and a recruitment pulse, especially when the rainfall is above average (Erfanzadeh et al., 2016; Weber-Grullon et al., 2020). Overgrazing not only reduces understory vegetation production and cover but also changes the composition from grass to unpalatable forb-dominated herbaceous communities (Erfanzadeh et al., 2016). Even in water-limited ecosystems, high atmospheric CO_2 by increasing water use efficiency and fertilization facilitates an increase in shrub cover and biomass (Stevens et al., 2016; Mndela et al., 2022a). Shrub proliferation is more prevalent in infrequently burned rangelands with low browsing ungulate densities (Dreber et al., 2019), as this promotes an increase in shrub cover and root biomass, thereby intensifying shrub–grass competition for light and below-ground resources (Van Zyl and Avenant, 2018).

Shrub encroachment causes biodiversity loss and a decline in rangeland and livestock productivity, adversely affecting the local economy (Anadon et al., 2014; Wieczorkowski and Lehmann, 2022) and pastoralist's livelihoods (Liao et al., 2018; Hare et al., 2021). In South Africa, a dwarf shrub, *Seriphium plumosum* (L.) Thunb. (Asteraceae) previously known as *Stoebe vulgaris*, has encroached vastly in grassland and savanna biomes (Urban et al., 2021). The encroachment of this shrub was first noticed early 1920s in Southern Africa, after which its abundance increased abruptly (Clark et al., 2020). An increase in *S. plumosum* encroachment characterizes degradation (Wepener, 2007) and is partly driven by the high production of wind-dispersed seeds together with high recruitment success in nutrient-poor soils (Snyman, 2012).

S. plumosum both competes with understory plants and limits germination and establishment *via* allelopathy (Snyman, 2010). Nonetheless, the legacy effects of the *S. plumosum* allelopathy following shrub control are transient, with its autotoxicity persisting only for 12 to 16 weeks in the soil (Van Zyl and Avenant, 2018). This presents a great opportunity for herbaceous vegetation restoration through shrub control. Various shrub control methods have been proposed including chemical, burning, and mechanical measures (Avenant, 2015; Pule et al., 2023). These control measures have different efficacies (Marquart et al., 2022) and impose differential effects on the herbaceous plant diversity, cover, and production (Nkosi et al., 2018; Clark et al., 2020; Graham et al., 2020). Thus, herbaceous vegetation responses following shrub control need to be ascertained from short- to long-term temporal scales.

A plethora of research has been conducted on *S. plumosum* control (Snyman, 2012; Clark et al., 2020; Marquart et al., 2022); however, none of these studies assessed long-term vegetation responses above 3 years. This limits our understanding of the long-term outcomes of shrub control on understory vegetation. Monitoring long-term vegetation responses to shrub control is important to devise appropriate vegetation restoration management (Mndela et al., 2022b). In most studies, e.g., Marquart et al. (2022), shrub control has never been integrated with herbivory to mimic the ideal scenarios where ungulates are an integral part of the ecosystem. This questions the reliability and practicality of the results obtained from such studies for biodiversity conservation and vegetation restoration. Ungulates through browsing and trampling open shrub canopies for herbaceous plant recruitment (O'Connor et al., 2020). Furthermore, ungulates play a crucial role in reducing shrub seedling recruitment (Hare et al., 2021) and resprouting of partially killed shrubs, thereby minimizing re-encroachment (Venter et al., 2017).

A comprehensive study that considers holistic responses of herbaceous vegetation to integrated management of *S. plumosum* is crucial (Nkosi et al., 2018). This study, therefore, investigates herbaceous plant responses after 7 years following the integration of chemical and mechanical shrub control with herbivory. The objective of the study was to assess the long-term impacts of shrub control on herbaceous vegetation and determine how wild ungulates modulate herbaceous vegetation responses to shrub control.

2 Materials and methods

2.1 Site description

The study was conducted at Telperion Nature Reserve (TNR) close to the town of Bronkhorstspruit in the Mpumalanga Province of South Africa (Figure 1). The reserve is 11,000 hectares in size and is 1,350 m above sea level. The reserve is used mainly for the conservation of populations of wild ungulates including Plains zebra, Blue and black wildebeest, Red hartebeest, Eland, Springbok, Kudu, Gemsbok, Waterbuck, and Blesbok (Table 1; Roux, 2017). The stocking rate of the wild ungulates at TNR is 0.20 large stock unit/ha (MacFadyen, 2014). The mean annual rainfall at TNR ranges from 650 to 700 mm per year, with the highest rain received during the summer months around January (Graham et al., 2020). The average minimum and maximum temperatures are 7°C and 27°C, respectively. The reserve comprises grasslands, wetlands, mosaics of woodlands on the ridges, forest in the valleys, and the free-flowing Wilge River, which supports wild ungulates through forage provision, drinking, and insulation against heat. The main vegetation type at TNR is Rand Highveld Mesic Grassland, with the largest parts being classified as *Eragrostis curvula*–*S. plumosum* midslope plateau grassland (Brown et al., 2022). The common grass species are *Themeda triandra*, *Elionurus muticus*, and *Tristachya leucothrix* (Mucina et al., 2006). *S. plumosum* encroaches heavily with the highest density of 9,500 plants/ha (Graham et al., 2020) and a mean canopy cover of 50.0% ± 8.9% where ungulates are present to 83.8% ± 6.3% where ungulates are absent (Figure 2). The shrub cover was on average 80% across the plots before shrub control. In 2022, the shrub cover in 50% removal treatment was 25% and 68% in non-enclosures and enclosures, respectively, and these were 2- and 1.2-fold lower than shrub cover in no removal treatments (Figure 2;

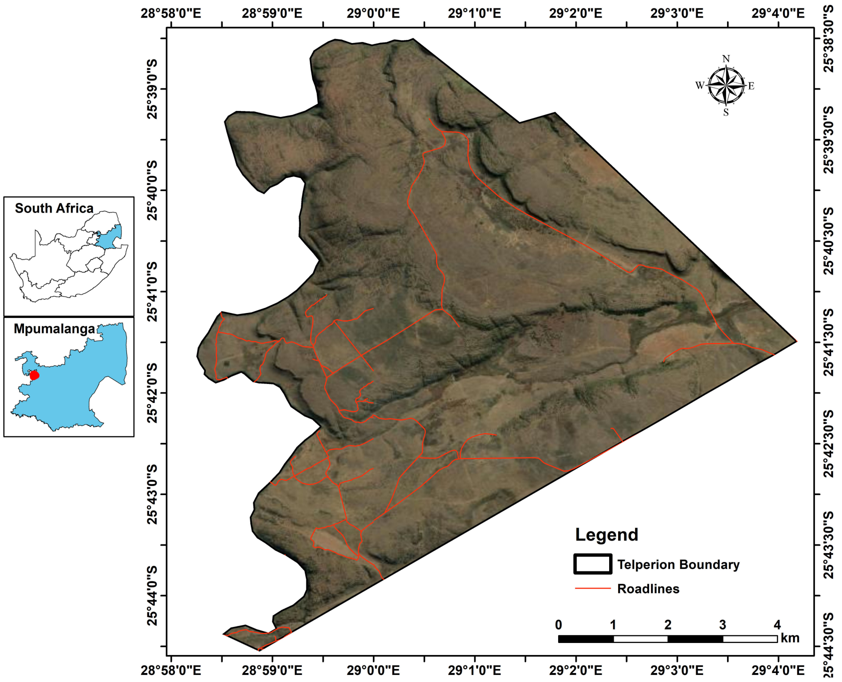

FIGURE 1
Map showing the location of Telperion in Mpumalanga Province of South Africa.

TABLE 1 Wild ungulate species and their feeding habits and diet composition.

Animal species		Feeding habit$^{\varphi}$				
Common name	Scientific name	CGR	BGR	BR	IF	Diet composition
Eland	*Tragelaphus oryx*				✓	Grasses constitute 18%, and the rest is woody plant material, e.g., twigs, leaves, and pods[1]
Blue wildebeest	*Connochaetes taurinus*	✓				Grasses constitute 95% of the diet mainly during wet season and only small proportion of woody material[2]
Blesbok	*Damaliscus pygargus*	✓				Grasses constitute 84%, and the other portion is constituted by browsing
Black wildebeest	*Connochaetes gnou*	✓				Grasses constitute 95%, and the species browse occasionally when grass production is low[1]
Red hartebeest	*Alcelaphus buselaphus*	✓				Grasses constitute 87%, and the other portion is constituted by browsing[2]
Plains zebra	*Equus quagga*		✓			Depends largely on grazing, with C4 grasses constituting 89% of the diet[2]
Gemsbok	*Oryx gazella*				✓	Grasses constitute 88%, but the species browse when grass forage is scarce[1]
Waterbuck	*Kobus ellipsiprymnus*	✓				A sole grazer, with grasses constituting 92% of the diet[2]
Impala	*Aepyceros melampus*				✓	Grasses constitute approximately 52% of the diet, and the rest is woody plant material[1]
Kudu	*Tragelaphus strepsiceros*			✓		Grasses constitute as small as 4% of the diet, with the largest portion constituted by woody plant material[1]
Springbok	*Antidorcas marsupialis*				✓	Grasses constitute approximately 17% of the diet, and the largest proportion is constituted by browsing of woody plants[2]

CGR$^{\varphi}$, concentrate grazers; BGR$^{\varphi}$, bulk grazers; BR$^{\varphi}$, browsers; IF$^{\varphi}$, intermediate feeders.

[1] Cerling et al. (2003).

[2] Venter and Kalule-Sabiti (2016).

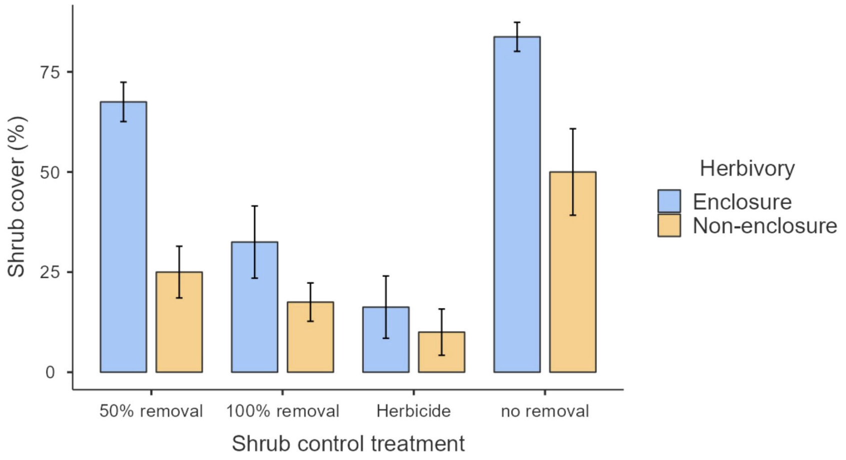

FIGURE 2
Shrub cover across different shrub control methods within enclosures and non-enclosures.

Supplementary Table 1). The soil types characterizing the reserve are sandy soils derived from Quartzite of the Witwatersrand Supergroup, Pretoria group, and the Selons River formation of the Rooiberg group (Mucina et al., 2006).

2.2 Experimental design

Four spatially distributed sites were located at TNR. At each site, a 50 × 25-m area was demarcated and divided into two paired 25 × 25-m plots, with one plot fenced to preclude wild ungulates (enclosure) and the other plot left open to wild ungulates (non-enclosure; Table 2). A 1.5-m-high wire mesh was erected to prevent access of medium- to large-sized ungulates to enclosures. Thus, the enclosures were only accessible to small mammals including rodents and lagomorphs. The wild ungulates kept in the reserve and their feeding regime (Mentis, 1981) and diet composition (Venter et al., 2017; Cerling et al., 2003) are presented in Table 1. Five ungulates are grazers, two are browsers, and four are intermediate feeders (Table 1). More than 80% of the diet of grazers is C4 grasses, whereas 82%–96% diet of browsers consists of woody plant twigs, pods, and leaves (Table 1).

Following a split-plot design, each enclosure or non-enclosure was subdivided into sixteen 4 × 4-m subplots, for which each of the following shrub control treatments was assigned randomly in four subplots: foliar herbicide, 50% shrub removal, 100% removal, and no removal (untreated controls) (Nkosi et al., 2018). The subplots were interspaced by 1.5 m to avoid spillover effects of shrub control treatment to another. A 2-m wide buffer was maintained around the main plot to account for the edge effect. Collectively, enclosures and non-enclosures are loosely referred to as herbivory treatment in this study.

2.3 Shrub control treatments

The mechanical treatment, which included 50% and 100% shrub removal, was conducted by cutting and grubbing the above-ground stems and rhizomes of *S. plumosum* stems (Nkosi et al., 2018). Since the shrub is rhizomatous, cutting the above-ground stem only would lead to resprouting, which, therefore, justifies pulling out rhizomes from the soil by grubbing in 50% and 100% removal treatments (Snyman, 2012). For 50% shrub removal, half of the *S. plumosum* individuals in each subplot were removed, whereas all *S. plumosum* plants were removed for the 100% removal treatment. For the herbicide treatment, metsulfuron-methyl herbicide was applied at a concentration of 4 g/L of water by spraying the photosynthetic foliage of *S. plumosum* using knapsack sprayers. Metsulfuron-methyl was selected owing to its known efficacy in shrub control (Marquart et al., 2022) and its high selectivity against non-target plants when applied to the foliage (Du Toit, 2012). This is a systematic herbicide that is translocated to plant parts below ground (Spencer, 2012), making it the most relevant to control rhizomatous shrub species. To avoid the pre-emergent effects of the herbicide on the soil-stored seeds, shrub control treatments were applied during the 2015 growing season long after seedling recruitment (Nkosi et al., 2018).

2.4 Data collection

Vegetation was assessed in October at the end of the spring season of 2022 after 7 years of the establishment of shrub control and herbivory experiment. Three 1-m^2 quadrats were sampled in two opposite corners and at the center of each subplot, giving a total of 384 quadrats. All plants encountered in each quadrat were identified to species level using the nomenclature by Van Oudtshoorn (1999) for grasses and Van der Walt (2009) for forbs, legumes, shrubs, and sedges. The minimum and maximum basal diameters were measured at the 3-cm stubble height of each plant encountered in each quadrat using a standard ruler. For creeping plants, each above-ground shoot was identified as an independent plant when the distance between shoots was >10 cm (Davies et al., 2012). All individuals encountered in each 1-m^2 quadrat were used to estimate plant density, whereas the total

TABLE 2 The study design indicating shrub control treatments within enclosures and non-enclosures across three experimental sites.

	Enclosure				Non-enclosure			
Site 1	NR	MH	50%	100%	50%	100%	MH	NR
	50%	100%	NR	MH	NR	MH	50%	100%
	MH	50%	100%	NR	100%	50%	NR	MH
	100%	NR	MH	50%	MH	NR	100%	50%
	Non-enclosure				Enclosure			
Site 2	100%	NR	MH	50%	NR	50%	100%	MH
	NR	50%	100%	MH	MH	100%	50%	NR
	MH	100%	50%	NR	100%	NR	MH	50%
	50%	MH	NR	100%	50%	MH	NR	100%
	Enclosure				Non-enclosure			
Site 3	50%	100%	NR	MH	100%	MH	NR	50%
	MH	NR	50%	100%	50%	NR	100%	MH
	NR	MH	100%	50%	MH	100%	50%	NR
	100%	50%	MH	NR	NR	50%	MH	100%
	Non-enclosure				Enclosure			
Site 4	MH	50%	100%	NR	50%	100%	MH	NR
	100%	MH	NR	50%	NR	MH	50%	100%
	50%	NR	MH	100%	100%	50%	NR	MH
	NR	100%	50%	MH	MH	NR	100%	50%

NR, no removal; MH, metsulfuron-methyl herbicide; 50%, 50% shrub removal; 100%, 100% shrub removal.

number of different species per quadrat was used as the estimate of species richness. Plant density was divided into graminoids (grasses and sedges) and non-graminoids (forbs and rushes). The herbaceous cover was estimated in each subplot as a collective proportion of graminoids, forbs, and rushes. The plant cover was estimated visually in the whole subplot by two researchers, and the estimates were later averaged to obtain a single representative cover. The basal cover was calculated as the total ellipsoid area of all basal crowns of plants per quadrat and expressed as a proportion of the area of a quadrat. The ellipsoid area was calculated from the minimum and maximum basal diameters.

2.5 Statistical analysis

All analyses were conducted in JASP statistical software. Two-way analysis of variance (ANOVA) was performed in a split-plot design, with enclosures and/or non-enclosures (n = 2) and shrub control treatments (n = 4) included as the main plots and subplots, respectively. Generalized linear mixed-effects models (GLMEMs) were fitted to determine the fixed effects of herbivory, shrub control treatments, and their interactions on herbaceous cover, basal cover, species richness, diversity, and plant density. Experimental sites were added as random factors in the GLMEMs. For species richness and plant density, plant functional groups (graminoids and non-graminoids) were further included as the additional independent variable to assess three-way interactions between herbivory, shrub control, and plant functional groups. The species diversity was calculated using the Shannon–Wiener diversity index (H′) according to Magurran (2004), as follows (Equation 1):

$$\mathrm{H}' = -\sum_{i=1}^{S} P_i \ ln\ P_i \qquad (1)$$

where S is the number of species in each subplot and P_i is the relative abundance of species i.

When the interactions were significant at α = 0.05, a Tukey's *post-hoc* test was used to conduct multiple mean comparisons.

3 Results

3.1 Herbaceous plant canopy and basal cover

Herbivory ($F_{1,\ 128}$ = 31.24, p < 0.001), shrub control ($F_{3,\ 128}$ = 21.11, p < 0.001), and herbivory by shrub control interaction ($F_{3,\ 128}$ = 2.83, p = 0.050) had significant effects on herbaceous canopy cover (Table 3). Non-enclosures had 3-fold and 4-fold higher herbaceous canopy cover compared to enclosures for 50% removal (t = 4.86, p <

TABLE 3 The F-test and *p*-values of the herbivory treatment, shrub control, plant functional groups (PFG), and their interactions on herbaceous vegetation indicators.

Dependent variable	Source of variation	F	*p*
Herbaceous plant cover	Herbivory	31.24	<0.001
	Shrub control	21.11	<0.001
	Herbivory × Shrub control	2.83	0.050
Basal cover	Herbivory	14.42	<0.001
	Shrub control	10.53	<0.001
	Herbivory × Shrub control	4.49	0.009
Species diversity	Herbivory	18.51	<0.001
	Shrub control	4.39	0.009
	Herbivory × Shrub control	1.26	0.301
Total species richness	Herbivory	19.08	<0.001
	Shrub control	7.15	<0.001
	Herbivory × Shrub control	3.29	0.031
Total plant density	Herbivory	22.86	<0.001
	Shrub control	4.51	0.008
	Herbivory × Shrub control	3.59	0.022
Species richness for plant functional groups	Herbivory	15.36	<0.001
	Shrub control	4.69	0.005
	Herbivory × Shrub control	3.03	0.036
	Plant functional group (PFG)	113.81	<0.001
	PFG × Herbivory	13.34	<0.001
	PFG × Shrub control	3.24	0.028
	PFG × Herbivory × Shrub control	0.71	0.548
Plant density for plant functional groups	Herbivory	12.01	<0.001
	Shrub control	3.71	0.016
	Herbivory × Shrub control	3.17	0.030
	Plant functional group	95.46	<0.001
	PFG × Herbivory	14.16	<0.001
	PFG × Shrub control	2.85	0.044
	PFG × Herbivory × Shrub control	1.92	0.135

0.001) and no removal treatments (t = 3.62, p = 0.018), respectively (Figure 3A). In non-enclosures, the shrub control treatments had similar herbaceous canopy cover, with herbicide treatment exhibiting higher herbaceous cover (t = 3.20, p = 0.050) than no removal treatment (Figure 3A). In enclosures, 100% removal and herbicide treatments attained similar herbaceous canopy cover (t = 0.07, p = 1.000), which was 3 to 6-fold higher than in the 50% removal and no removal treatments (Figure 3A).

The herbivory ($F_{1,\ 128}$ = 14.42, $p < 0.001$), shrub control ($F_{3,\ 128}$ = 10.53, $p < 0.001$), and herbivory by shrub control interaction ($F_{3,\ 128}$ = 4.49, p = 0.009) had a significant effect on basal cover (Table 3). Basal cover (BC) was 4-fold and 2-fold higher in non-enclosures relative to enclosures for 50% removal (t = 3.60, p = 0.019) and 100% removal treatments (t = 3.36, p = 0.034), respectively (Figure 3B). Herbicide treatment had a significant 3- to 5-fold higher basal cover compared to other shrub control treatments in enclosures ($p < 0.001$; Figure 3B).

3.2 Species diversity

Herbivory ($F_{1,\ 128}$ = 18.51, $p < 0.001$) and shrub control ($F_{3,\ 128}$ = 4.39, p = 0.009), but not their interaction ($F_{3,\ 128}$ = 1.26, p = 0.301), had a significant effect on species diversity (Table 3). The 50% removal and no removal treatments attained a significantly higher diversity in non-enclosures than enclosures (Figure 4A). The 100% removal and herbicide treatments had comparable diversity in enclosures and non-enclosures (Figure 4A). Generally, shrub control treatments exhibited a similar diversity of 1.70 (±0.24) on average in non-enclosures, whereas herbicide treatment had a significantly higher diversity ($p < 0.05$) of 1.60 (±0.17) compared to 50% removal (0.76±0.17) and no removal treatments (0.63±0.17) in enclosures (Figure 4A).

3.3 Species richness

Species richness was significantly affected by herbivory ($F_{1,\ 128}$ = 19.08, $p < 0.001$), shrub control ($F_{3,\ 128}$ = 7.15, $p < 0.001$), and their interaction ($F_{3,\ 128}$ = 3.29, p = 0.031; Table 3). Species richness was similar ($p > 0.05$) between non-enclosures and enclosures for all shrub control treatments except 50% removal, which had significant (t = 4.54, p = 0.001) 3-fold more species in non-enclosures than in enclosures (Figure 4B). On average, shrub control treatments had eight species in non-enclosures, which were 3-fold more than species recorded in 50% removal and no removal treatments in enclosures (Figure 4B).

A three-way interaction between herbivory, shrub control, and plant functional groups (PFGs) was not significant (Table 3). Shrub control by PFG ($F_{3,\ 128}$ = 3.24, p = 0.028) and herbivory by PFG ($F_{1,\ 128}$ = 13.34, $p < 0.001$) interactions were significant for species richness (Table 3). For all shrub control treatments, the species richness of graminoids was significantly higher than that of non-graminoids ($p < 0.01$; Figure 5A). Graminoid richness in 100% removal and herbicide treatments was similar but significantly higher compared to that in 50% removal and no removal treatments (Figure 5A). There were more graminoid species in non-enclosures than enclosures ($p < 0.001$) and even three times more than non-graminoids in both enclosures and non-enclosures (Figure 5B).

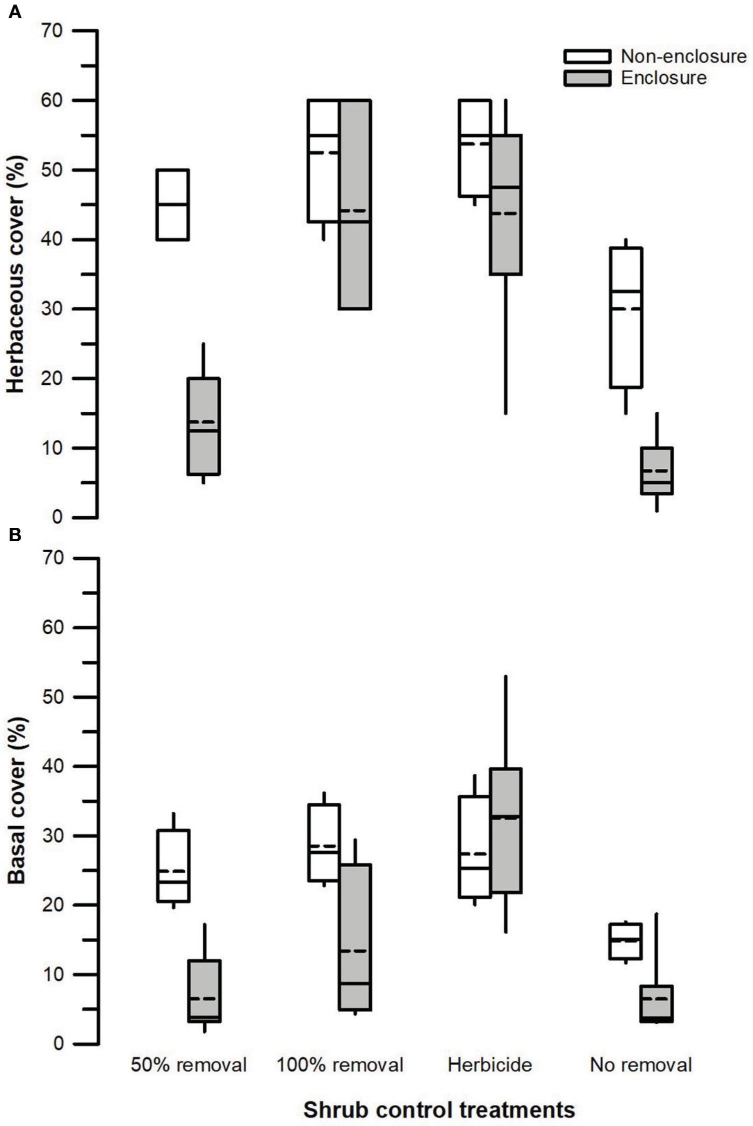

FIGURE 3
Herbaceous canopy cover **(A)** and basal cover **(B)** across different shrub control treatments in enclosures and non-enclosures. Bold dotted and undotted lines inside the box denote the mean and median, respectively, and the lower and upper limits of the box denote 25th and 75th quartiles, respectively. The lower and upper whiskers are minimum and maximum values, respectively.

3.4 Plant density

The herbivory ($F_{1,\ 128}$ = 22.86, p < 0.001), shrub control ($F_{3,\ 128}$ = 4.51, p = 0.008), and their interaction ($F_{3,\ 128}$ = 3.59, p = 0.022) had a significant effect on the total plant density (Table 3). The plant density was significantly higher (t = 4.39, p = 0.002) in non-enclosures relative to enclosures for 50% removal (Figure 6). All shrub control treatments had similar plant densities in non-enclosures, but these densities were 4-fold higher than for 50% removal and no removal treatments in enclosures (Figure 6).

A three-way interaction of the herbivory, shrub control, and PFGs was not significant for plant density (Table 3). Nonetheless, shrub control by PFG ($F_{3,\ 128}$ = 2.85, p = 0.044) and herbivory by PFG interactions ($F_{1,\ 128}$ = 14.16, p < 0.001) significantly affected plant density (Table 3). Graminoids had higher densities than non-graminoids in 100% removal (t = 2.95, p = 0.049) and herbicide treatment (t = 2.95, p < 0.001; Figure 5C). When graminoids were compared across shrub control treatments, herbicide treatment attained a 2-fold higher density than the 50% removal (t = −4.10, p = 0.003) and no removal treatment (t = 4.14, p = 0.002; Figure 5C). However, graminoid density was nearly 2-fold more in non-enclosures than enclosures and 7-fold more in non-graminoids in both enclosures and non-enclosures (Figure 5D).

4 Discussion

Our results revealed that herbaceous canopy cover and basal cover responses depended largely on the interactive effects of herbivory and shrub control, indicating that herbivory had

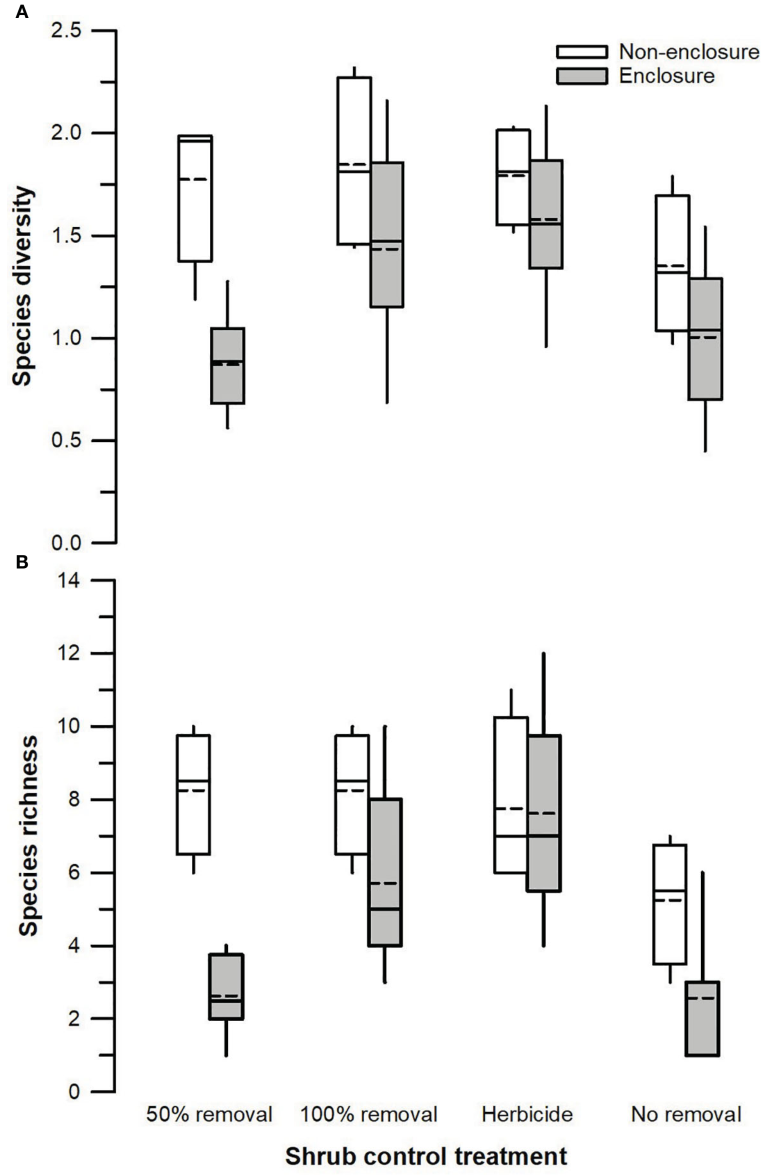

FIGURE 4
Species diversity **(A)** and total species richness **(B)** across different shrub control treatments in enclosures and non-enclosures. Bold dotted and undotted lines inside the box denote the mean and median, respectively, and the lower and upper limits of the box denote 25th and 75th quartiles, respectively. The lower and upper whiskers are minimum and maximum values, respectively.

additive effects. These effects were more apparent in the 50% shrub removal and no removal treatments (Figure 3), largely due to ungulates, which reduced shrub cover further in non-enclosures (Figure 2; Supplementary Table 1). For 50% removal treatment particularly, wild ungulates reduced shrub cover to 25%, which is below a 40% encroachment threshold identified by Roques et al. (2001) for encroached rangelands of Southern Africa (Figure 2). Generally, if shrub cover increases above 40%, herbaceous cover and density decline due to competition for light and below-ground resources in the semi-arid savannas of Southern Africa (Roques et al., 2001). Thus, the shrub–grass competition is expected to be minimal in 50% removal treatment in non-enclosures, given that shrub cover was nearly 2-fold less than the threshold. These responses were due to wild ungulates in non-enclosures that opened shrub cover, thereby increasing herbaceous plant cover, basal cover, and plant density in the 50% removal to similar levels as the 100% removal and herbicide treatments. This result is attributable to browsing and trampling by wild ungulates, which break shrub twigs and open shrub cover further, subsequently enhancing herbaceous plant recruitment and establishment (O'Connor et al., 2020). This was affirmed by plant density response trends, which resembled herbaceous cover responses (Figure 6), with densities responding more positively in non-enclosures that received 50% removal relative to 100% removal and herbicide treatments. These results signified that the integration of wild ungulates and shrub control facilitated plant colonization in non-enclosures, probably by creating a microclimate favorable for plant regeneration and recruitment.

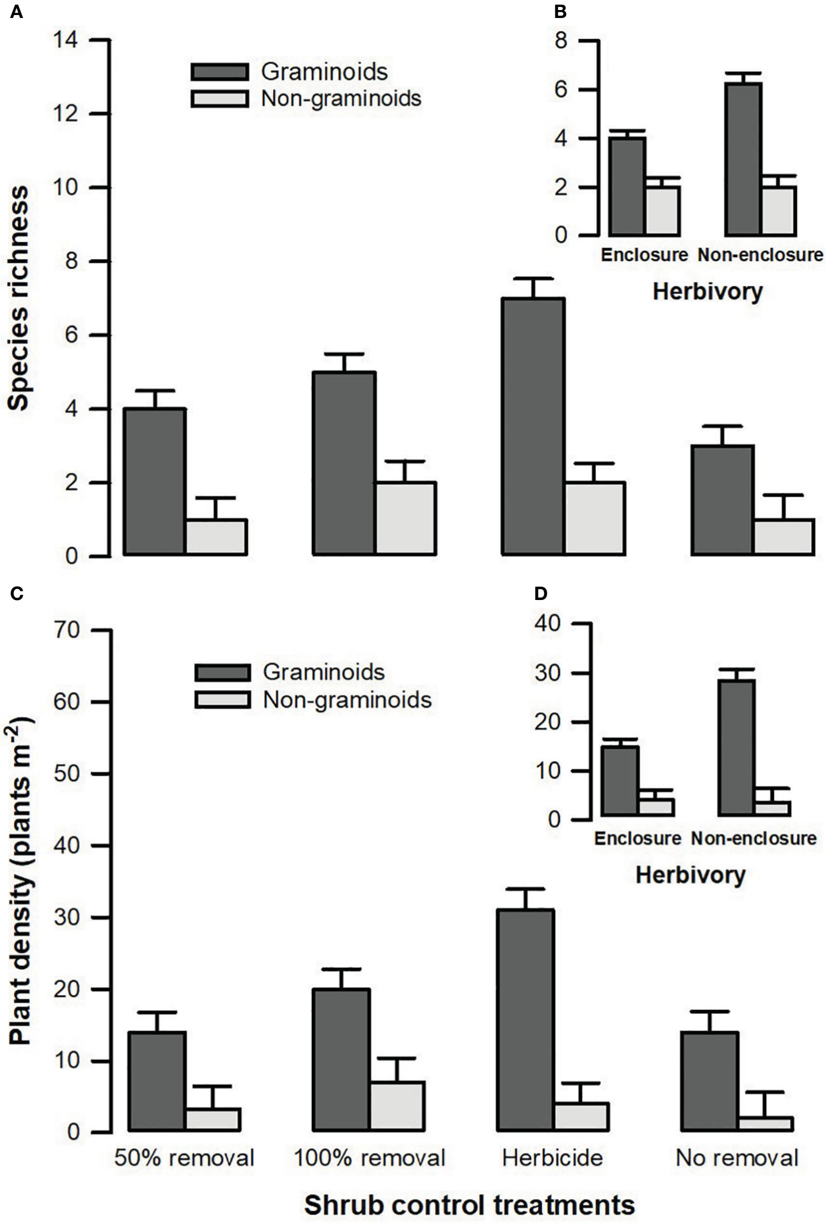

FIGURE 5
Species richness **(A)** and plant density **(C)** of different plant functional groups across shrub control treatments and between enclosures **(B)** and non-enclosures **(D)**. The bars indicate the mean ($\bar{X}$), and the error bars indicate the standard error.

A low herbaceous plant cover in enclosures for 50% removal treatment was probably due to shrub cover recovery due to the absence of ungulates to control resprouting. *S. plumosum* exerts serious competitive effects (Snyman, 2012; Marquart et al., 2022), with shading from shrub canopy reducing leaf production, leading to low herbaceous plant cover (Mndela et al., 2022c). In contrast to previous studies (e.g., Stokely et al., 2020), we found higher plant cover in herbicide treatment regardless of the herbivory treatment. Our findings concur with Marquart et al. (2022), who recorded higher herbaceous plant cover in plots where *S. plumosum* was treated with metsulfuron-methyl. This herbicide is highly selective against non-target herbaceous plants (Du Toit, 2012) and generally achieves a 100% mortality of *S. plumosum* (Marquart et al., 2022), though a minor shrub recovery of 10% and 16% cover occurred in non-enclosures and enclosures, respectively, in this study (Figure 2; Supplementary Table 1). Since metsulfuron-methyl was applied during summer long after several rains, seedling recruitment and establishment were not interrupted; hence, plant density and cover were the highest in shrub-cleared treatments.

Herbaceous cover responses to herbicide and 100% removal treatment were similar (Figure 3), and this was not surprising, given that shrub cover recovery was minimal after 7 years in these treatments (Figure 2; Supplementary Table 1). Hence, graminoid densities were the highest in the herbicide and 100% removal treatments compared to 50% removal and no removal treatments (Figure 5). This finding indicates that graminoids, largely grasses,

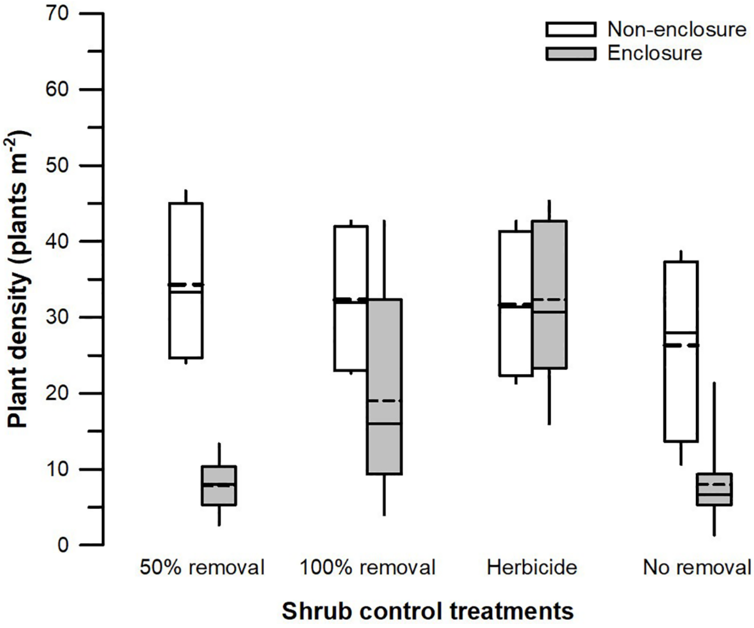

FIGURE 6
Plant density across different shrub control treatments in enclosures and non-enclosures. Bold dotted and undotted lines inside the box denote the mean and median, respectively, and the lower and upper limits of the box denote 25th and 75th quartiles, respectively. The lower and upper whiskers are minimum and maximum values, respectively.

are more vulnerable to *S. plumosum* encroachment and that a reduction in shrub cover created habitat conditions favorable for grass colonization. Generally, a reduction in shrub cover triggers an increase in seed production by graminoids, contributing greatly to herbaceous plant recruitment (Bakker et al., 2014; Mndela et al., 2020). The increase in graminoid densities is a result of increased light availability to the understory layer and a release from shrub competition for soil nutrients and moisture (Haussman et al., 2016). This was further underpinned by the interaction between plant functional groups and herbivory treatment, with graminoid density responding more positively to wild ungulates in non-enclosures where shrub cover was low for all treatments. A reduction in shrub cover increases the decomposition and N positively of organic material due to increased temperatures and microbial activity (Ward et al., 2015). This, therefore, increases organic matter and nutrient availability, thereby creating safe sites for plant recruitment and establishment. Since the clearing of shrubs allows the dispersal of seeds from nearby areas into cleared sites, dispersed seeds together with those produced by local vegetation colonize vigorously in nutrient-rich patches following shrub control (Mndela et al., 2022b; Mndela et al., 2022c).

Furthermore, we found that species diversity responded similarly in enclosures and non-enclosures, more so for 100% removal and herbicide treatments (Figure 4), highlighting that herbivory had a marginal effect on species diversity in these treatments. As a result, for both 100% removal and herbicide treatments, diversity was not different from that of 50% removal in non-enclosures. Generally, habitat heterogeneity in 100% removal and herbicide treatments is low due to the removal of almost all shrubs (Nkosi et al., 2018); hence, higher species richness did not translate to higher diversity in these treatments than in the 50% removal treatment. This is ascribed to the dominance of a few species, which led to these few species homogenizing vegetation in the 100% removal and herbicide treatments. Certain herbaceous species adapted to high light conditions tend to monopolize space, exploit resources, and eliminate late colonizers following shrub control (Mndela et al., 2022a).

5 Conclusions

This study was designed to provide a mechanistic understanding of how integration of shrub control and herbivory affected herbaceous vegetation after 7 years of a one-off shrub management event. The results revealed that herbaceous vegetation responses with regard to plant cover, density, and richness depend on the interactions between herbivory and shrub control. Herbivory effects were more apparent in the 50% shrub removal treatment signifying that wild ungulates had additive effects on the herbaceous vegetation responses. This suggests that ungulates should be considered an integral part of the management plan for *S. plumosum* encroachment in mesic grasslands. Although the 50% removal treatment had lower graminoid richness than the 100% removal and herbicide treatments, species diversity together with herbaceous plant cover and density remained comparable between the former and latter two treatments. Overall, our results suggest that apart from herbicide treatment, the integration of 50% removal and herbivory holds great promise for the restoration of *S. plumosum*-encroached mesic grasslands. The use of 50% shrub removal combined with wild ungulates is not only ecologically significant but also economically viable relative to 100% shrub removal. The results of this study are a basis for the management and conservation of herbaceous vegetation diversity and productivity for sustainable wildlife production.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

MM: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. AB: Conceptualization, Writing – review & editing. LB: Conceptualization, Investigation, Resources, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1280157/full#supplementary-material

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Exploring the spatial distribution of social impacts in protected areas

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Protected Areas (PAs) are the most widely applied tool for biodiversity conservation. The primary role of these areas is to protect and restore ecosystems, but it has become increasingly evident that in order to designate effective PAs it is also crucial to take into consideration how they contribute to sustainable local socio-economic targets. In the past decade studies focusing on social impacts of PAs have increasingly studied a number of impacts such as on people's quality of life, income and connectedness to nature. Although the literature on social impacts of PAs has increased there is limited evidence regarding the distribution of these impacts across different locations inside and near PAs. Addressing this gap is useful for practitioners considering that it is now widely accepted that social impacts are a significant predictor for the level of public support for PA. In the current study we explore this topic and analyse the spatial distribution of perceived social impacts in 4 European Protected Areas using primary data from 1,251 households. We apply a new modeling framework using Bayesian statistics revealing that social impacts are often unevenly distributed between local communities and extend outside the boundaries of a PA. Our analysis also shows that spatial proximity with other people (what are the perceptions of people who live nearby) is more important for predicting most perceived social impacts of PAs compared to how close respondents are to a PA. Our results highlight that social impacts may be geographically unevenly distributed in PAs and we present a new way of measuring the spatial distribution of these impacts which can be useful for national park authorities and in general managers of PAs.

KEYWORDS

national parks, spatial autocorrelation, Bayesian statistics, nature conservation, social effectiveness, Peak District, Eifel

1 Introduction

The Designation of Protected Areas (PAs) is the most important policy internationally for the protection of biodiversity. According to the International Union for the Conservation of Nature (IUCN) a PA *is a clearly defined geographical area, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values* (Day et al., 2012). At an international level, approximately 17% of terrestrial and inland water areas and 8% of coastal waters and the ocean consist of PAs (UNEP, 2021).

Europe is the region in the world with proportionally the highest number of PAs (European Environment Agency, 2017). Currently, it is estimated that approximately 22.7% of land and 8.25% of water is protected in the region under a mosaic of designations such as the NATURA 2000 network (areas listed under both the Habitats and Birds Directives 92/43/EEC, 2009/147/EC), the Ramsar convention and nature reserves (https://biodiversity.europa.eu/protected-areas/coverage-representativity). Despite the wide designation of PAs, human pressures on biodiversity remain significant in the European region (Mammides et al., 2020). To address this challenge the new EU Biodiversity Strategy for 2030 states that PAs will remain an instrumental policy tool for the protection of biodiversity in the European region having also a significant role for the mitigation of the adverse impacts of climate change (European Commission, 2020). Specifically, the strategy aims to conserve 30% of the land area and 30% of the sea area in the European Union in line with the Kumnig-Montreal Global Biodiversity Framework (https://www.cbd.int/gbf/).

Although PAs were initially designed as a policy tool to protect biodiversity, it is now widely recognised that their role should be much broader and PA management plans need also to promote local socio-economic priorities. This is because the ecological and social effectiveness of PAs is closely interconnected (Ban et al., 2019).

One of the most important obstacles in designating effective PAs is the lack of consideration of social impacts. Although PAs can have significant positive social impacts, including beneficial effects on health and wellbeing (Romagosa, 2018; Burdon et al., 2019; Rodrigues et al., 2022) they can also have social costs for certain groups in the local communities living inside or near their borders (Jones et al., 2020a). The designation of PAs often introduces fundamental changes to local and regional economies and societies, such as restrictions on fishing and logging activities (Lockwood, 2010; Brandt et al., 2015; Schreckenberg et al., 2016; Campbell et al., 2017; Ban et al., 2019; Bennett et al., 2019). These negative impacts on local communities often results in inefficient PA management (Rife et al., 2013) where locals ignore PA regulations resulting in significant damage to biodiversity.

Following the Convention of Biological Diversity and Aichi target 11 (CBD, 2020) several studies focused on issues of social equity in PAs (Franks et al., 2018; Zafra-Calvo et al., 2019), emphasizing the need to conduct subjective assessments of social impacts (capturing perceived social impacts) (Bennett et al., 2019; Jones et al., 2020b) and explore how these impacts are distributed between different stakeholders (de Lange et al., 2016; Oldekop et al., 2016). Social impacts are important as they are closely linked with the level of public support for PAs with higher benefits resulting in higher levels of acceptance (Bennett et al., 2019; Buta et al., 2014; McGinlay et al., 2023).

Despite the increase of studies on this topic, there is very limited evidence regarding the spatial distribution of impacts within a PA and thus there is a lack of evidence regarding whether benefits and costs of PAs are distributed in an equitable manner across different communities living near or inside a PA. An existing study has found that living near a PA has a positive effect on wellbeing levels in countries in the Global South (Naidoo et al., 2019). Furthermore, Jones et al. (2020b) found that an individual's location in the PA is an explanatory parameter for people's wellbeing level. Going beyond these two publications, no study currently exists that explores how social impacts of PAs are distributed across different communities and what are the key factors explaining spatial variations of social impacts. A key question that remains unclear is whether PAs are equitable from a spatial perspective or are there issues with the distribution of social impacts? As a result of the lack of studies there is also no suggested methodology in the literature on how to assess the spatial distribution of social impacts.

This is an important area of research considering that PAs are primarily a spatial policy tool with a geographical focus (IUCN, 2008). Specific boundaries of the PA are set within which certain restrictions exist for locals. In this study, we contribute to this line of enquiry and explore whether the location of residents in a PA along with other social factors influence the outcomes people perceive as a result of a PA. These include the impact of the PA on their personal income, their quality of life, their involvement in recreational activities, how well they are connected to nature and their relations with other members of the local community. In order to explore potential links between people's location and perceived social impacts we propose a new modeling framework utilizing data from 1,251 structured questionnaires distributed to local residents of four European PAs.

2 Methods

2.1 Data collection

In order to explore the spatial distribution of perceived social impacts we collected primary data using structured questionnaires from four PAs between 2020-2021: Prespes National Park (Greece), Pieniny National Park (Slovakia), Eifel National Park (Germany) and Peak District National Park (United Kingdom) (Figure 1).

The four PAs were selected based on the following criteria: a) areas that have local communities living inside their boundaries; b) areas that are large enough to allow the exploration of spatial distribution; c) areas that are designated as National Parks and managed mainly by the state so that when comparing the results the governance framework is similar; d) areas that are in Europe as they fall under similar legislative framework.

Data on perceived social impacts of residents of the PAs were solely related to impacts of specific the PA each respondent resides and not to other remaining protected areas.

In all research areas, the sampling frame included those who live inside the PA or within a 10 km buffer zone around the PA boundary. The specific distance from the borders of the PAs was inspired by previous research (Oldekop et al., 2016; Naidoo et al., 2019) arguing that the distance of 10 km could be considered the threshold at which PAs can exert socio-economic impacts to residents. Details of the research areas, the sampling frame, the sample and the mean of survey distribution are available in Table 1. Due to the low response rate expected in online surveys the sample invited to participate to these surveys was much higher compared to the one of the face to face surveys.

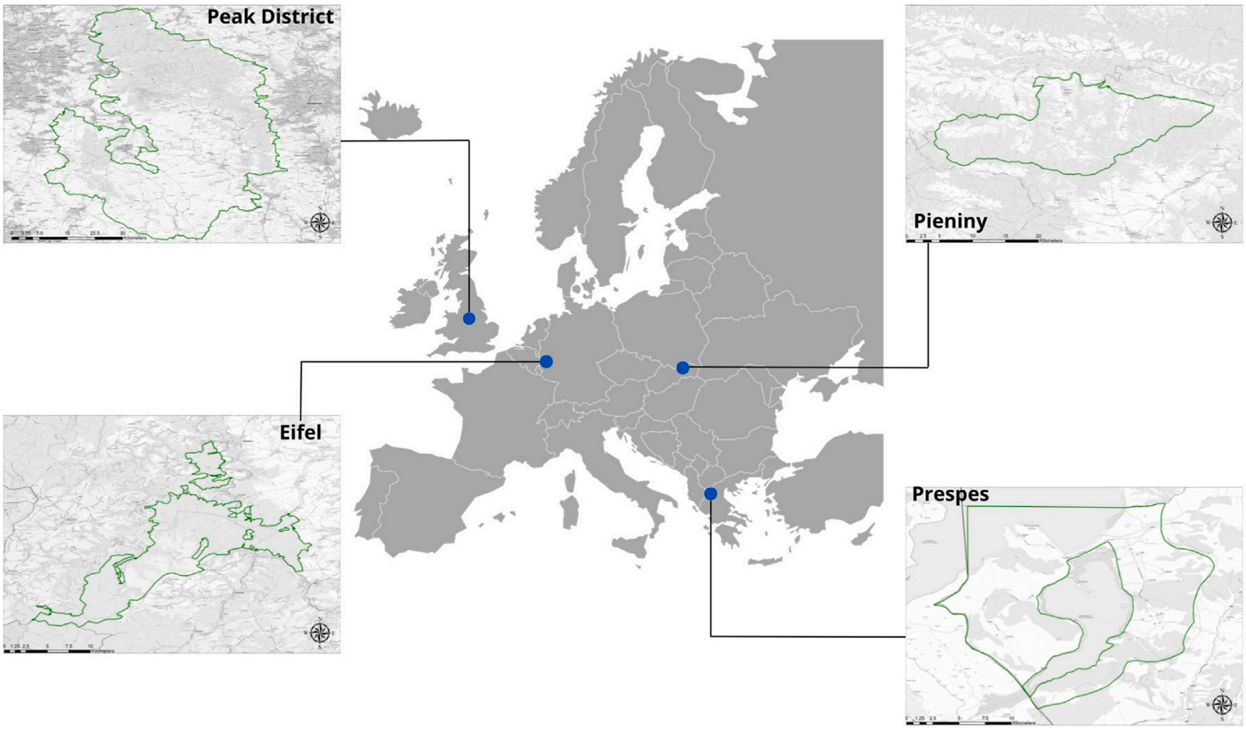

FIGURE 1
Location of the case study areas.

TABLE 1 Characteristics of PAs and details of distribution process.

	Type of PA, size in km^2	Year of establishment	Socio-economic activities	Approximate sampling frame	Sample invited to participate	Final sample	Distribution
Research area							
Pieniny	Terrestrial (37.5)	1967	Tourism and recreation, logging, agriculture	2,000	500	223	Face to face (2021)
Eifel	Terrestrial and wetland (110)	2004	Tourism and recreation, logging	6,000	6,000	309	Online (by invitation)
Prespes	Terrestrial and wetland (195)	2003	Tourism and recreation fishing, agriculture	2,000	400	308	Face to face (2020)
Peak District	Terrestrial (1,438)	1951	Tourism and Recreation agriculture	44,000	4,000	411	Online (by invitation)

2.2 Questionnaire description

The questionnaire captured perceptions about social impacts of the PA, socio-economic attributes and the location of the individual. We explored perceptions of 5 types of social impacts: Personal income, quality of life, recreation, connectedness to nature and social relations. These were considered to be the most frequent impacts noted in PAs in Europe based on a recent literature review (Jones et al., 2020b).

Geographical coordinates of local residents' were used to capture the location of the respondents at village/town level (i.e., urban areas within or at a maximum of 10 km distance from borders of PAs). Regarding the independent variables a number of socio-economic indicators were captured which have been identified in the literature as potential determinants of people's perceptions of PAs (Table 2). These included: a) place attachment (Lin and Lockwood, 2014); b) subjective wellbeing (Jones et al., 2020b); c) trust in institutions managing the PA (Cherry et al., 2018; Bennett et al., 2019); d) demographics (gender, age, education and income) and e) personal socio-environmental values (Stern et al., 1999; Lopez-Mosquera and Sanchez, 2012; Wynveen et al., 2015). A detailed description of dependent variables (impacts) and independent variables is provided in Table 2.

TABLE 2 Description of dependent variables (impacts) & independent non-spatial variables.

	Category	Question		Scale of measurement
Dependent variables	Social impacts	How has the designation of the PA impacted you regarding the following issues in the past years?	Personal Income	5-point Likert scale: 1-very negative impact, 5- very positive impact, 3- neutral/no impact
			Your quality of life	
			Your involvement in recreational activities	
			Social relations with locals	
			Your connectedness to Nature	
Non-spatial independent variables	Place attachment **(Block A)**	Place attachment	This area means a lot to me	5-point Likert scale: 1-lowest level of agreement, 5-highest level of agreement
	Subjective wellbeing **(Block B)**	Level of satisfaction with quality of life	I am satisfied with my quality of life	5-point Likert scale: 1-lowest level of agreement, 5-highest level of agreement
	Trust in institutions **(Block C)**	Trust in governance institutions: How much do you trust the following institutions	PA Management Authority	5-point Likert scale: 1-lowest level of trust, 5-highest level of trust)
			Local government	
	Sociodemographics **(Block D)**	Demographics	Gender	Categorical: Male/Female/Other
			Education	Categorical: Primary, Secondary and Vocational, Higher Education
			Age	Categorical (1: 18-25; 2: 26-35; 3: 36-45; 4: 46-55; 5: 56-65; 6: 66+)
			Income	Categorical: No income, Low, Middle, High
	Values **(Block E)**	Values: Which degree of importance do you attach to the following values in your life?	Respecting the Earth	5-point Likert scale: 1-lowest degree of importance, 5-highest degree of importance
			Being Helpful to others	
			Being influential	
			Equal opportunities for all	
			Being wealthy	
			Unity with nature	

2.3 Data analysis

We developed a detailed methodological framework in order to explore the spatial distribution of social impacts in the PAs and also investigate whether spatial aspects may influence perceived social impacts (see also Figure 2).

Step 1: We first examined overall spatial effects through the calculation of Global Moran's *I* statistic of spatial autocorrelation which is frequently used for ecological data (Beguin et al., 2012; Gaspard et al., 2019; Legendre, 1993; Lichstein et al., 2002). In this study Moran's *I* are used to estimate if one respondent's perceptions of social impacts are similar/dissimilar to the perceptions of social impacts of other respondents located nearby or whether location does not play any role at all. A detailed description of the Global Moran's *I* statistic process is included in Supplementary Appendix SB. In particular, we calculated global Moran's (for the complete datasets) and local Moran's *I* statistic (for sub-regions within each PA) for a more refined examination of existence of spatial autocorrelations in the data.

Step 2: Spatial maps were created, using ArcGIS, visualizing the distribution of impacts across different areas and the estimated Moran's values. To identify the location of potentially significant clusters, constructed spatial maps were also created. All spatial maps for the visualization of the spatial clustering of perceived impacts in the study areas were constructed with the use of QGIS software (QGIS Development Team, 2015). Further details regarding the construction of the maps are available in Supplementary Appendix SB2.

Step 3: Bayesian regression spatial modeling was used for the in-depth investigation of different spatial effects including the role of respondent's location in relation to the PA and the role of spatial proximity between local residents regarding their views of perceived impacts. The former type of spatial information was measured through

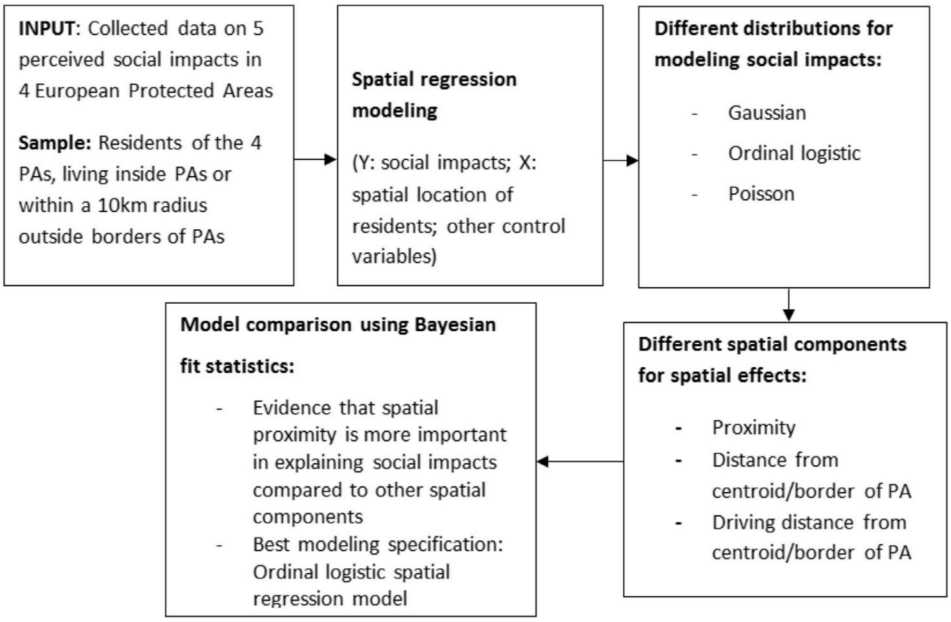

FIGURE 2
Step-by-step description of methods of the current study.

TABLE 3 Description of spatial variables used as predictors of impacts.

Spatial variables	Description
Spatial proximity	The average distance (in km) of each resident from other local residents in each PA
Euclidean distance from centroid of PA	The straight line distance (in km) from the centroid of the highest protection zone to the centroid of the urban area* where each respondent is located
Euclidean distance from border of PA	The straight line distance (in km) from the border of the highest protection zone to the centroid of the urban area where each respondent is located
Driving distance from centroid of PA	The driving distance (in km) from the centroid of the highest protection zone to the centroid of the urban area where each respondent is located
Driving distance from border of PA	The driving distance (in km) from the border of the highest protection zone to the centroid of the urban area where each respondent is located
Driving time from centroid of PA	The driving time (in min) from the centroid of the highest protection zone to the centroid of the urban area where each respondent is located
Driving time from border of PA	The driving time (in min) from the border of the highest protection zone to the centroid of the urban area where each respondent is located

(*) Urban areas: villages/small towns located within the boundaries of the PAs, or at a maximum distance of 10 km outside the geographical boundaries of the PAs.

two distinct distances (measured in km): the distance (Euclidean and driving) from the centroid of the protected area and the distance (Euclidean and driving) from the border of the protected area. In addition, we estimated the driving distance (km) and driving time (in minutes) of each resident to the centroid/border of their protected area. Euclidean distance between residents was also utilized. Table 3 presents the different spatial variables included in the model.

Step 4: In this last step, a two-stage modelling approach was followed. Initially models were fitted including non-spatial independent variables to explain social impacts of respondents (these variables are presented in detail in Table 2). Then, upon selecting the statistically significant independent non-spatial variables, spatial measures were added in the models to explore the simultaneous effect of spatial and non-spatial information on social impacts. We used Bayesian statistics and employed suitably chosen regression models that combine both typical explanatory variables along with spatial information that is included in the models in the form of spatial components. Due to few missing data in certain variables, a multiple imputation (MI) methodology was applied, which is considered one of the most reliable processes for handling missing data in multivariate analysis (Rubin, 1996; Schafer and Graham, 2002). To perform MI, the SPSS MI module was utilized (IBM Corp. Released, 2020).

To model the social impacts of PAs, we used a set of explanatory variables (see Table 2). The selected predictor variables were included in the regression modeling as blocks, based upon the associations of

TABLE 4 Average impacts for the 4 PAs (standard deviation in parentheses).

PA	Impact on personal income	Impact on quality of life	Impact on recreational activities	Impact on connectedness to nature	Impact on social relations
Eifel	3.13	3.76	3.84	3.99	3.35
	(0.50)	(0.99)	(1.14)	(0.95)	(0.67)
Peak District	3.59	4.71	4.57	4.75	4.45
	(1.01)	(0.69)	(0.86)	(0.63)	(0.80)
Pieniny	3.23	3.78	3.81	3.89	3.41
	(0.68)	(0.83)	(0.84)	(0.89)	(0.79)
Prespes	2.99	3.66	3.63	3.81	3.10
	(1.02)	(1.11)	(1.13)	(1.19)	(1.13)

All questions were measured on a 5-point Likert scale with 1 representing very negative impact, 3 'no impact' and 5 'very positive impact'/benefit.

certain variables to each other. We compared the performance of three modelling specifications under the wider family of Generalized Linear Models (GLMs) (Gaussian, Poisson and a logistic regression model with a logit link function). In all models the dependent variables were the five impacts, and predictors were the 5 blocks of predictors (A, B, C, D and E) (Table 2). Using a forward stepwise process, where each block of independent variables is added in the previous regression model, we select the best fitted model to the data. At a next stage, we analyzed the relationship between social impacts and spatial dependence using a variety of distance measures by means of the generalized regression modeling (GLM) approach and the best selected models of the 6 blocks of control variables following the Bayesian paradigm (Lindley, 1983). All analyses were carried out using the WinBUGS software (Lunn et al., 2000).

A detailed description of statistical regression models utilized for our analysis is included in Supplementary Appendix SB3.

3 Results

3.1 Social impacts

Regarding perceived social impacts all 5 impacts measured in the questionnaire were considered beneficial by respondents or as having no impact with average scores being over or very close to the average score of 3. Table 3 presents the mean score for each impact in each PA. Impact on income was considered as the least positive in all study areas compared to the other four impacts. Higher benefits were recorded in the Peak District National Park (Table 4) where 4 out of the 5 impacts had an average score over 4.

3.2 Spatial distribution of social impacts

The global Moran's values indicated a positive and statistically significant (p-value<0.1) spatial autocorrelation ($I > 0$) for most impacts (Table 5). This result reveals significant spatial dependence in the majority of perceived social impacts in all PAs of our study. In the next sections we present the spatial distribution of impacts in each case study. We also include one example map for each case study visualising the average distribution of one impact along with the average local Moran's I values for each sub-region (Figures 3-6). Maps for the remaining impacts are included in the Supplementary Appendix SC.

3.2.1 Eifel National Park

In Eifel National Park, all impacts were evaluated above the mean value of the Likert scale, revealing several benefits for local communities. Most important positive impact was connectedness to nature followed by quality of life. In terms of spatial variation, there were similarities in the responses of participants especially in areas where people thought that the benefits were not as important (compared to other areas of the national park) (Figure 3). Furthermore, respondents in the South and East of the park and in one area in the North perceived more benefits for their quality of life. In terms of impact on recreation, areas where higher scores were noted also tended to be dissimilar. Areas with lower benefit scores, such as areas that are enclosed by the park, had high positive local Moran's I suggesting that respondents share their views (responses were more similar on these locations).

3.2.2 Peak District National Park

In the Peak District, overall, respondents perceive significant benefits from the existence of the park. This is more evident for the impact of the park on Quality of Life, Recreation and Connectedness to Nature (Table 4). Regarding similarity of values within locations our results show that there is a tendency for these values to be similar in areas where people perceive higher benefits on personal income (Figure 4). Higher values for the impact on quality of life correlate with a slight level of similarity between respondents. No spatial variation was noted for connectedness to nature whereas impact on social relations tended to be more beneficial in the north, central and east regions of the park. However, these areas tend to have dissimilar values where the lowest impact average area has the highest level of similar values.

3.2.3 Pieniny National Park

In Pieniny National Park urban communities, such as Spisska Stara Ves, had higher perceived social impacts overall. Impact on Quality of Life was the most important benefit according to respondents (Table 4). In terms of spatial variations, impact on income and social relations values tend to be similar across the locations of the park (Figure 5). In the remaining three impacts (Quality of Life, Recreation and Connectedness to Nature) the local Moran's I values tend to suggest higher dissimilarity between locations.

TABLE 5 **Moran's *I* global index along with corresponding significances for each social impact in each PA.**

Protected Area	Income	Quality of life	Recreational activities	Connectedness to nature	Social relations
Eifel	n.s	0.051***	0.116***	0.055***	n.s
Peak District	n.s	n.s	n.s	−0.066**	n.s
Pieniny	n.s	0.062**	n.s	0.061**	n.s
Prespes	0.070***	n.s	0.125***	0.104***	0.067***

[a]Index significant at 10% significance level, ** 5% significance level, *** 1% significance level; n. s.: Non-significant spatial autocorrelation.

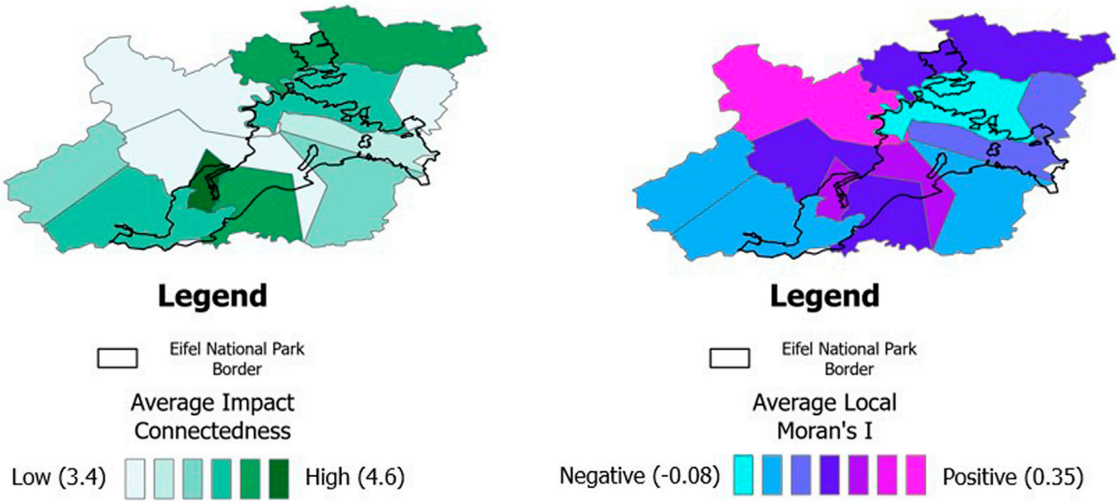

FIGURE 3
Spatial distribution of connectedness to nature in Eifel National Park (alongside local Moran's *I* results).

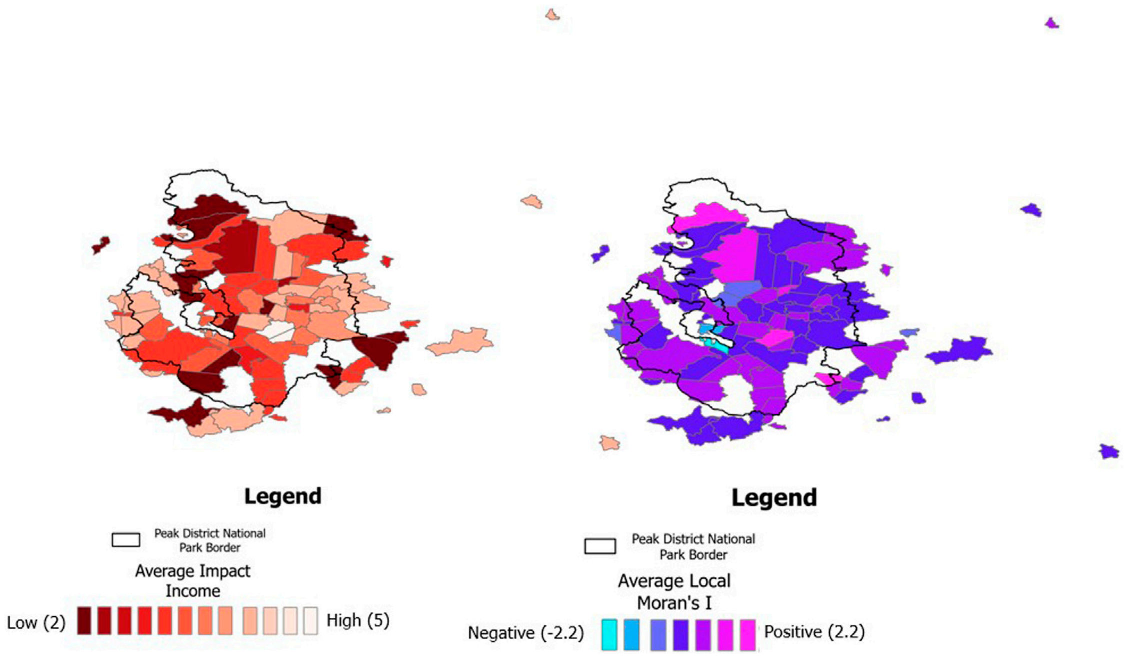

FIGURE 4
Spatial distribution of impact on personal income in the Peak District National Park (alongside local Moran's *I* results).

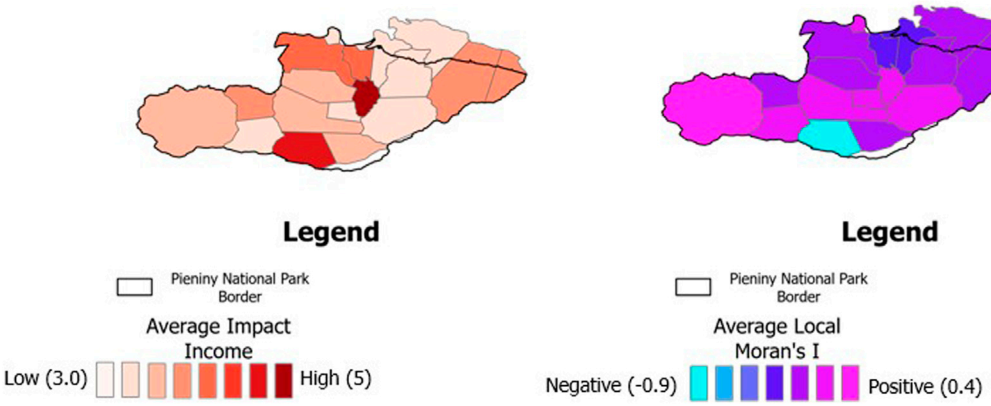

FIGURE 5
Spatial distribution of impact on personal income in Pieniny national park (alongside local Moran's *I* results).

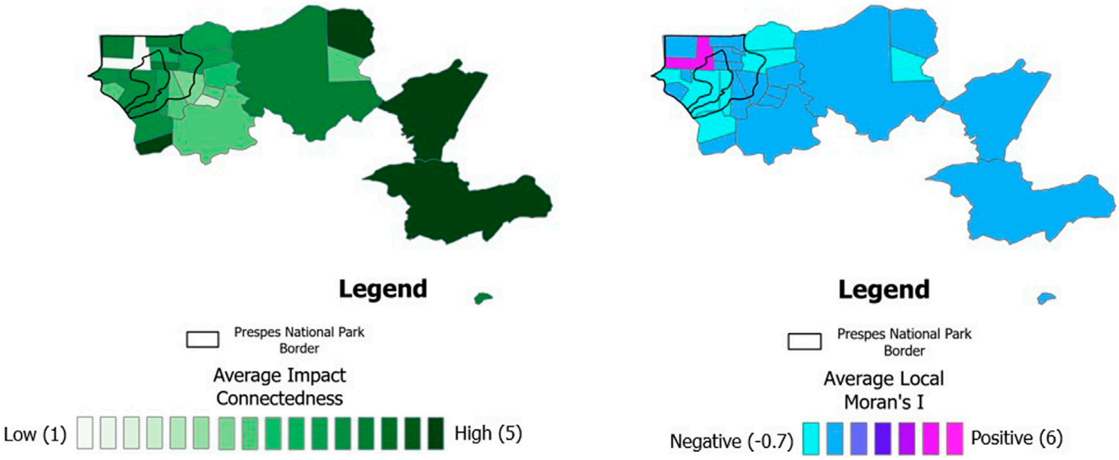

FIGURE 6
Spatial distribution of connectedness to nature in Prespes national park (alongside local Moran's *I* results).

3.2.4 Prespes National Park

In Prespes National Park social impacts were evaluated lower compared to the other 3 sites of our study (Table 4) with lowest values noted for impact on income. In the north-west of the park, on the shore of lake Prespa, low impact scores are noted with high spatial similarity. On the contrary, respondents from the eastern parts of the park noted higher benefits but there is more specific pattern of spatial similarity or dissimilarity. This suggests a high level of variation in the impact effect across the different social indicators.

3.3 The effect of spatial and non-spatial parameters on perceived social impacts

We completed a two-stage analysis to select the statistically significant non-spatial independent variables and then at a second stage we add the three spatial components to select between them the best indicator. This process allowed us to select the best model that includes the best performed non-spatial and spatial independent components.

3.3.1 Effect of non-spatial parameters

Results of the best model fit in terms of distributional specification for the response variables, utilizing the non-spatial independent indicators (first stage of step 4 in our methodology including the non-spatial variables) are included in the Supplementary Appendix Tables SA3, 4. Inspection of the model fit outputs reveals that Poisson regression gives the most parsimonious results in terms of variable selection, with this modeling specification providing the smallest number of statistically significant predictors when compared to other choices. Upon selecting the best regression models for the prediction of the five impacts, given by the ordinal logistic models fitted to the data, we can see that in all cases, all predictors are statistically significant (see Supplementary Appendix Tables SA2.

Table 6 presents the estimated median coefficients for the best selected models for each social impact, based upon the goodness-of-fit

TABLE 6 Parameter estimates (median values) along with 95% credible intervals (in the parentheses) for the statistically significant covariates in the best selected regression models for the five perceived social impacts.

Covariate	Impact on personal income	Impact on quality of life	Impact on recreational activities	Impact on connectedness to nature	Impact on social relations
	Parameter estimate (95% credible interval)	Parameter estimate (95% credible interval)	Parameter estimate (95% credible interval)	Parameter estimate (95% credible interval)	Parameter estimate (95% credible interval)
Constant	n.s	3.56 (0.26, 4.91)	n.s	n.s	2.48 (1.67, 3.89)
Place attachment (A)	0.31 (0.16, 0.44)	0.61 (0.47, 0.75)	0.48 (0.35, 0.61)	0.62 (0.48, 0.77)	0.42 (0.29, 0.56)
Subjective wellbeing (B)	0.57 (0.39, 0.71)	0.55 (0.39, 0.69)	0.31 (0.16, 0.43)	0.37 (0.23, 0.53)	0.41 (0.27, 0.55)
Trust MA (C1)	n.s	0.41 (0.29, 0.53)	0.39 (0.27, 0.51)	0.46 (0.34, 0.59)	0.34 (0.23, 0.46)
Trust government (C2)	−0.13 (−0.25, −0.02)	−0.21 (−0.32, −0.10)	−0.16 (−0.26, −0.04)	−0.27 (−0.39, −0.15)	−0.12 (−0.23, −0.03)
Gender (ref. category: Female)					
Male	n.s	n.s	n.s	n.s	n.s
Age (ref. category: 65+)					
18-25	n.s	n.s	n.s	n.s	−1.25 (−1.82, −0.67)
26-35	−0.59 (−1.12, −0.08)	−1.25 (−1.78, −0.73)	−0.54 (−1.06, −0.05)	−0.85 (−1.43, −0.29)	−0.74 (−1.23, −0.26)
36-45	n.s	−0.98 (−1.44, −0.51)	−0.52 (−0.99, −0.07)	−0.56 (−1.07, −0.07)	−0.91 (−1.33, −0.50)
46-55	n.s	−0.83 (−1.31, −0.35)	n.s	−0.55 (−1.08, −0.05)	−0.53 (−0.96, −0.10)
56-65	n.s	−0.62 (−1.12, −0.11)	n.s	n.s	n.s
Education (ref. category: Higher education)					
Primary level	n.s	−1.09 (−1.56, −0.64)	−0.89 (−1.35, −0.42)	−1.15 (−1.61, −0.67)	−0.64 (−1.11, −0.16)
Secondary and vocational	n.s	−0.43 (−0.68, −0.18)	−0.31 (−0.55, −0.07)	−0.38 (−0.64, −0.13)	n.s
Income (ref. category: High)					
None	n.s	n.s	n.s	n.s	n.s
Low	n.s	n.s	n.s	n.s	n.s
Medium	n.s	n.s	−0.37 (−0.68, −0.06)	−0.41 (−0.71, −0.08)	n.s
Respect Earth (E1)	0.21 (0.04, 0.41)	0.37 (0.16, 0.53)	0.44 (0.25, 0.62)	0.39 (0.20, 0.61)	0.31 (0.12, 0.51)
Unity (E2)	n.s	n.s	−0.19 (−0.37, −0.02)	n.s	n.s
Helpful (E3)	n.s	n.s	n.s	0.22 (0.04, 0.39)	0.25 (0.04, 0.45)
Equality (E4)	n.s	n.s	n.s	0.25 (0.09, 0.41)	−0.20 (−0.38, −0.03)
Influential (E5)	n.s	n.s	n.s	n.s	n.s
Wealthy (E6)	n.s	−0.22 (−0.36, −0.09)	n.s	n.s	−0.16 (−0.29, −0.02)

n.s.: Non-significant parameter.

selection. It is noted that among the most important non-spatial predictors of social impacts are “Place attachment” and “Subjective wellbeing”, both affecting positively and significantly all social impacts. Personal environmental values indicator is positively associated with all perceived impacts. Positive connection in four out of the five impacts were found for trust in the management authority of the park. It is interesting though that trust in the national government is associated with perceived social impacts in a negative way.

Respondents aged 26–35 years had the most negative perceptions on social impacts, in comparison to citizens of all other age categories. Education was also a significant predictor of social impacts in four out of the five models, with people of lower

TABLE 7 Fit statistics for the best selected models with additional spatial components (in bold the lowest fit values indicating best fit for models including only statistically significant predictors).

Distance	Fit statistics	Impact on personal income	Impact on quality of life	Impact on recreational activities	Impact on connectedness to nature	Impact on social relations
Spatial proximity	Deviance	2,563	**2,525**	**2,785**	**2,420**	**2,774**
	DIC	2,589	**2,552**	**2,811**	**2,447**	**2,800**
Euclidean distance from centroid	Deviance	2,564	2,562	2,799	2,436	2,813
	DIC	2,590	2,589	2,825	2,462	2,839
Euclidean distance from border	Deviance	2,562	2,567	2,803	2,437	2,819
	DIC	2,587	2,594	2,829	2,463	2,845
Driving distance from centroid	Deviance	2,563	2,566	2,801	2,437	2,815
	DIC	2,588	2,592	2,827	2,464	2,840
Driving distance from border	Deviance	2,562	2,570	2,806	2,439	2,815
	DIC	2,588	2,597	2,832	2,467	2,842
Driving time from centroid	Deviance	2,561	2,570	2,806	2,439	2,815
	DIC	2,587	2,597	2,831	2,467	2,842
Driving time from border	Deviance	2,562	2,570	2,806	2,437	2,816
	DIC	2,589	2,597	2,833	2,465	2,842

educational levels generally perceiving lower benefits in comparison to respondents with a higher educational level. Other demographic, such as gender and income, did not seem to have a significant role in explaining variations of social impacts.

3.3.2 Results of a model exploring the effect of spatial and non-spatial components

Table 7 presents the results of model fit for the ordinal logistic regression as selected from the non-spatial analysis, with the addition of the various distance measures (spatial independent variables, Table 7). Our results reveal that spatial proximity between local residents is a better measure of spatial dependence for explaining variations in perceived impacts when compared to other types of spatial dependence, i.e., relative location and accessibility to the PA. This significant effect of proximity is clear on all impacts except for impact on income, where it seems that spatial effects are not important for its estimation (the inclusion of each one of the spatial variables either increases or keeps at the same levels goodness-of-fit statistics produced by the non-spatial regression models-differences in the DIC values are below the 3 units which is required for indication of statistical difference between fitted models).

When comparing the other three types of spatial distance (Euclidean and driving distance from centroid/border of PAs, driving time from centroid/borders), no large differences are observed.

The Euclidean distance from the centroid of the PAs results to models with a better fit compared to other type of distances for all impacts apart from income. This is an indication that the location of respondents in relation to the centroid of a PA is more important compared to accessibility to the national park (measured with driving distance and driving time in our study).

As a final assessment of model performance, for the best selected spatial models for the five impacts we assessed predictive performance visually by constructing spatial maps combining the observed values of impacts with their predictive values as obtained by the spatial regression modeling. Figure 7 compares observed with predicted values for the impacts on income and connectedness to nature. Blue points in the graphs indicate a good predictive performance (observed value falls within the 95% credible intervals of prediction), whereas red points indicate poor performance (observed value falls outside the 95% credible intervals). According to these figures the impact on income spatial model presented the best fit to the data (Figure 7). Social relations, recreation and quality of life also predicted relatively good fit, with few exceptions of values falling outside the credible intervals. Connectedness to nature had the worst fit of all impacts. The performance plots for the rest of the impacts in each national park in our study have been included in the Supplementary Appendix SC.

4 Discussion

In this study we examined the geographical distribution of social impacts in four European Protected Areas as these are perceived by local communities. Our analysis explores how social impacts are distributed in different locations within or close to a PA and also whether the location of the respondent in relation to the boundaries of the PA influence their perceptions.

Our results show that there are differences on how social impacts are distributed across different communities living inside or very close to the boundaries of a PA. For example, in Pieniny National Park it was noted that urban communities (Spisska Stara

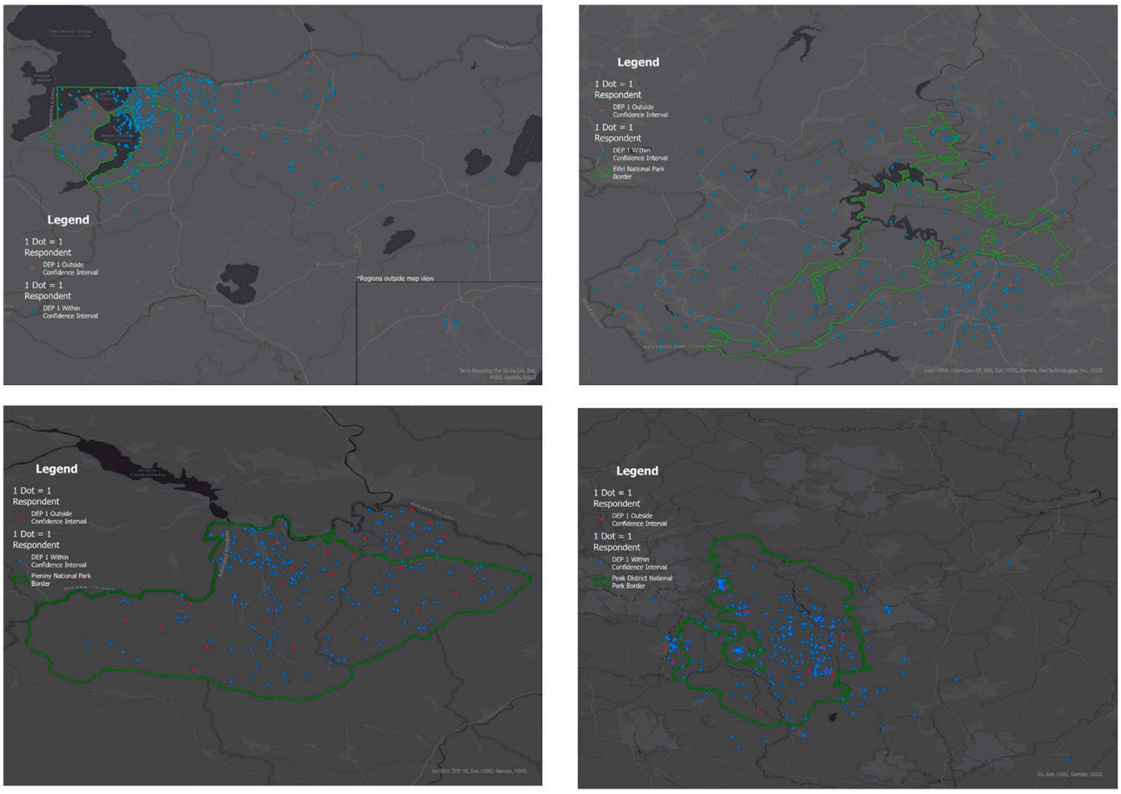

FIGURE 7
Predictive spatial maps for the 4 PAs for impact on income.

Ves) have higher perceived social impacts revealing a better appreciation of the contribution of the park on how they connect to nature and their quality of life. In Prespes National Park our results show that those who live closer to the park perceive lower benefits regarding certain impacts. These findings may reveal issues with uneven geographical distribution of social impacts in protected areas.

In order to understand why social impacts may be unevenly distributed we explored whether spatial differentiations in social impacts are attributed to the location of the individual (in relation to the boundaries of the PA) or whether this is explained by other social parameters. From the global and local Moran values analysis we note a significant spatial dependence in most perceived social impacts in the four PAs under study. Our results showed that proximity of respondents to each other is the most important determinant of perceived social impacts when compared to all 7 spatial measures included in the study, including proximity to the border and proximity to the centroid of the PA (average distance, straight line, driving distance). This result reveals that the proximity to the border of the PA determines to some extent how people perceive social impacts but a more important predictor are the perceptions of people who the respondent lives nearby. This was particularly evident in the case of negative perceptions as in areas where people tended to perceive lower benefits participants tended to have similar perceptions. This result was verified in the four out of the five impacts, with the exception of impact on income. It seems that when people consider impact of PAs on income, the spatial proximity is no longer a significant connecting factor for similar perceptions, in comparison to all other perceived impacts. This result may be explained considering that impact on income is expected to be closely linked with touristic activities and the location of specific infrastructure within a national park. Thus, perceptions may be influenced more by the proximity of economic activities rather than the community within which an individual lives and we would propose that additional research is conducted in this direction.

As proximity cannot be seen in isolation as an indicator explaining perceived social impacts we also tested whether other social parameters influence perceptions. We used indicators that have been highlighted in the literature as potential predictors of people's perceptions for PAs (Lopez-Mosquera and Sanchez, 2012; Steg et al., 2018; Lin and Lockwood, 2014; Wynveen et al., 2015; Cherry et al., 2018; Bennett et al., 2019; Jones et al., 2020b). Apart from location, one of the most important parameters explaining perceived social impacts was place attachment. This result is in line with findings from Buta et al. (2014) where place attachment was found to influence pro-environmental civic engagement beliefs for PAs (Buta et al., 2014). Another indicator influencing perceptions of social impacts in our study was the level of trust in the PA management authority with residents who trusted the park authorities perceiving higher benefits. This type of trust can be considered a governance indicator and has been linked to public acceptance for PAs in previous studies (Cherry et al., 2018; Bennett et al., 2019). A possible explanation is that trust is linked with transparency aspects in PA management (Gall and Rodwell, 2016;

Engen et al., 2018). Thus in cases where people feel that management authorities are transparent via channels of communication may also perceive higher benefits. These results can be helpful for practitioners when trying to explore the level of impacts of PAs as these are perceived by local communities.

When looking at the fit of the models we also noted that the location of the individual and social parameters contribute significantly in predicting all perceived impacts apart from Connectedness to Nature. A possible explanation is that connectedness to nature may not be linked directly to the location of the respondents in relation to a PA and its wider impacts compared to other social outcomes such as recreation and income.

These findings show that future research would benefit from exploring not only how impacts are distributed across different groups but also how these impacts are distributed within the geographical area of a PA and beyond its boundaries. This is an important topic considering that Aichi Target 11 in the Convention of Biological Diversity (CBD, 2020) highlights the need to consider issues of social equity and governance in PAs. In this context, social impacts play a central role but the majority of studies so far have focused on the distribution of impacts across different stakeholders (e.g., de Lange et al., 2016; Dawson et al., 2017). Since PAs are spatially designed and their social and economic restrictions are influenced by geographical boundaries policymakers would benefit, when attempting to address issues around social equity, to also consider that the designation of a PA will impact different areas of a PA in different ways. Our study provides a step-by-step methodological approach which can be useful for practitioners interested in capturing the spatial distribution of social impacts in their area.

5 Conclusion

In this study we explored the distribution of social impacts in four European PAs focusing on the spatial distribution of social impacts as these are perceived by local communities living near or inside PAs. We applied a new modeling framework using spatial autocorrelation analysis, spatial GIS mapping and Bayesian regression analysis taking into account three sources for spatial effects: spatial proximity between local residents, spatial distance from the centroid of a PA and distance from the border of a PA. Our analysis reveals that spatial proximity of respondents is more important for predicting perceived impacts of PAs than the other two types of spatial effects. Other social predictors of perceived impacts are place attachment, trust in institutions and an individual's subjective wellbeing confirming previous studies. We argue that apart from exploring the distribution of impacts across different stakeholders, practitioners may find useful to consider also the spatial distribution of these impacts across different geographical areas of a PA. Conducting social impact assessments with a spatial angle can be essential in order to plan interventions mitigating negative impacts in areas of PAs which can be considered more disadvantaged compared to others receiving a variety of benefits such as increase of income from tourism and direct access to recreational activities. Through such interventions practitioners can maximise nature's contributions to people across all areas of a PA leading also to higher levels of support for the designation of these areas.

Data availability statement

The datasets presented in this article are not readily available because We are restricted to sharing only secondary data due to ethics approvals by the ERC and Warwick University. Requests to access the datasets should be directed to nikoleta.jones@warwick.ac.uk.

Ethics statement

The studies involving humans were approved by the University of Cambridge and the University of Warwick respective ethics committee. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

All authors contributed to developing the main ideas and framework of the paper. CM, NJ, and AB. carried out the data analyses; CM, AB, NJ, JS, JM, and PD. contributed to the writing process. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

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Conservation status of Brazilian snakes inhabiting the Atlantic Forest of Northeastern Brazil

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Due to the high level of disturbance in natural ecosystems and the progressive loss of habitats resulting from anthropic occupation, biodiversity conservation represents one of the greatest challenges today. Red lists of threatened species are essential tools for identifying species at risk of extinction and guiding conservation efforts. In this study, we assessed the vulnerability to extinction of 55 snake species that occur in the Atlantic Forest of northeastern Brazil in Paraíba state. We developed vulnerability indices based on 12 factors known to influence the survival of snake populations. To analyze the threat profiles and relative risk levels within the snake community, we employed principal component analysis (PCA) and cluster analysis. Additionally, we compared our findings with existing red lists of threatened species. Our results reveal that only 18% of the snake fauna in this region is free of any threat. The aquatic species *Helicops angulatus* and *Oxyrhopus trigeminus* were the snakes that presented the lowest risk of extinction, while *Caaeteboia gaeli* and *Crotalus durissus* presented the highest risk of extinction. Two groups of species were considered non-threatened and five groups were considered threatened. Our study provides the first overview on the conservation status of snake species in the northern portion of the Atlantic Forest and contributes to a better evaluation of conservation planning for this group in the region.

KEYWORDS

Atlantic Forest, red listing, extinction risk, distribution, ecology

1 Introduction

Red lists of threatened species are created based on various attributes of species biology, as well as the threats to which species are susceptible. These lists aim to identify species at risk of extinction and guide conservation actions and resource allocation (Collar, 1996). One of the most widely recognized red lists is produced by the International Union for Conservation of Nature (IUCN). The IUCN criteria primarily rely on population parameter estimates (criteria A, C, and D1), distribution data (criteria B and D2), and the probability of extinction (criterion E) (IUCN, 2018). These criteria, while designed to be applied on a global scale, have inspired several other lists, which apply the procedure at the regional level (Gärdenfors et al., 2001). Although the IUCN criteria effectively assess the extinction risk for many species (Rodrigues et al., 2006), certain groups, such as reptiles, pose challenges due to limited knowledge about their population parameters. As a result, many reptile species are evaluated solely based on inferred distribution or remain unassessed (Böhm et al., 2013). This scarcity of data hinders the comprehensive assessment of reptile populations using the IUCN criteria. Therefore, alternative approaches may be necessary to address the unique challenges faced by reptiles and ensure their proper conservation assessment and management.

Snakes, among reptiles, face significant challenges in accurately assessing their vulnerability to extinction. This is primarily due to the limited knowledge about the natural history of most snake species, which can be attributed to their prolonged periods of inactivity, elusive behavior, and low population densities (Seigel, 1993). Consequently, applying the IUCN criteria to evaluate the extinction risks of snake species becomes highly challenging. Recognizing this, several studies have explored alternative parameters to assess the vulnerability of reptiles, including snakes. These studies have investigated various hypotheses concerning intrinsic factors such as body size, litter size, and dietary specialization, as well as extrinsic factors like climate change and illegal trade in species, to evaluate the extinction risk of snake species (Filippi and Luiselli, 2000; França and Araújo, 2006; Luiselli, 2009; Tomović et al., 2015). These alternative criteria offer valuable insights for prioritizing conservation actions, particularly when accurate distribution and population data are lacking, which is often the case for many Brazilian snake species.

In a study on the preservation and conservation status of biodiversity worldwide, Myers et al. (2000) proposed 25 priority areas for conservation, one of which is the Atlantic Forest. Even though it has undergone extensive fragmentation over a prolonged time, the Atlantic Forest still harbors astonishing biodiversity, with more than 8000 endemic species of vascular plants, amphibians, reptiles, birds, and mammals (Myers et al., 2000). In Brazil, this biome stretches from Rio Grande do Norte and Paraíba in the north to Santa Catarina and Rio Grande do Sul in the south. The northeastern region of Brazil, particularly the portion of the Atlantic Forest located north of the São Francisco River known as the Pernambuco Endemism Center (Yi et al., 2017), has considerable species richness, harboring at least 143 species of reptiles, 91 of which are snakes (Pereira-Filho et al., 2023). This region has experienced rapid degradation over the years due to historical economic priorities, notably brazilwood and sugar cane (Coimbra-Filho and Câmara, 1996), and is considered an ideal "scenario" as described by Tabarelli et al. (2002), for local, regional, and even global species extinctions to occur.

Situated amidst this challenging scenario, the Atlantic Forest of Paraíba state has endured significant losses, with only 5% of its original area remaining (CEPED, 2012). Despite these constraints, the Paraíba Atlantic Forest stands out as a region of considerable snake species richness, with 55 species documented to date (Pereira-Filho et al., 2017), three of them recently described, i.e. the coral snake, *Micrurus potyguara* (Pires et al., 2014), the blind snake, *Amerotyphlops arenensis* (Graboski et al., 2015), and the ground snake *Caaeteboia gaeli* (Montingelli et al., 2020). Given the exceptional species diversity coupled with extensive biome degradation, it becomes imperative to assess the conservation status of these snake species, as a significant portion of this fauna may be facing the threat of extinction.

Therefore, our objective was to evaluate the vulnerability to extinction of snake species occurring in the Paraíba Atlantic Forest, northeast Brazil, to analyze the main factors that may threaten the viability of populations, to classify species in groups vulnerable to specific threats, and to compare our results with existing red lists of threatened species.

2 Material and methods

2.1 Study area

Paraíba state is situated in the northeastern region of Brazil, sharing borders with Rio Grande do Norte, Pernambuco, Ceará, and the Atlantic Ocean (Figure 1). Within this region lies the Paraíba Atlantic Forest (PAF), encompassing a total area of 5,994 km^2, which corresponds to approximately 11% of the state's territory. The PAF spans across 63 municipalities, either fully or partially (SOS Mata Atlântica, 2018), and comprises diverse ecosystems, including forests, restinga (coastal woodland), and mangroves (Tabarelli et al., 2006).

In terms of climate classification, the region falls under the Köppen tropical wet and dry (As) climate category. It experiences rainfall predominantly during autumn and winter, with average temperatures of 26°C and an annual precipitation of approximately 1800 mm (CEPED, 2012). A total of 18 conservation units are in this region. Among these, the Área de Proteção Ambiental da Barra do Rio Mamanguape (14 640 ha) was established for sustainable use, and the Reserva Biológica Guaribas (4051 ha) for integral protection, stand out as the largest territories among these conservation units.

2.2 Threat factors

To assess the vulnerability of snake species within the Paraíba Atlantic Forest, we adopted a comprehensive approach inspired by previous studies conducted by Filippi and Luiselli (2000); França and Araújo (2006), and Tomović et al. (2015). These studies utilized ecological and geographic data to evaluate the conservation status of snakes in Italy, Brazil, and Serbia, respectively. Drawing from their methodologies, we employed a ranking method to generate vulnerability indices based on 12 factors known to influence the survival of snake populations.

To obtain the necessary data for classifying these threat factors, we conducted an extensive review of relevant literature, carried out fieldwork, and gathered valuable insights from the collection of the

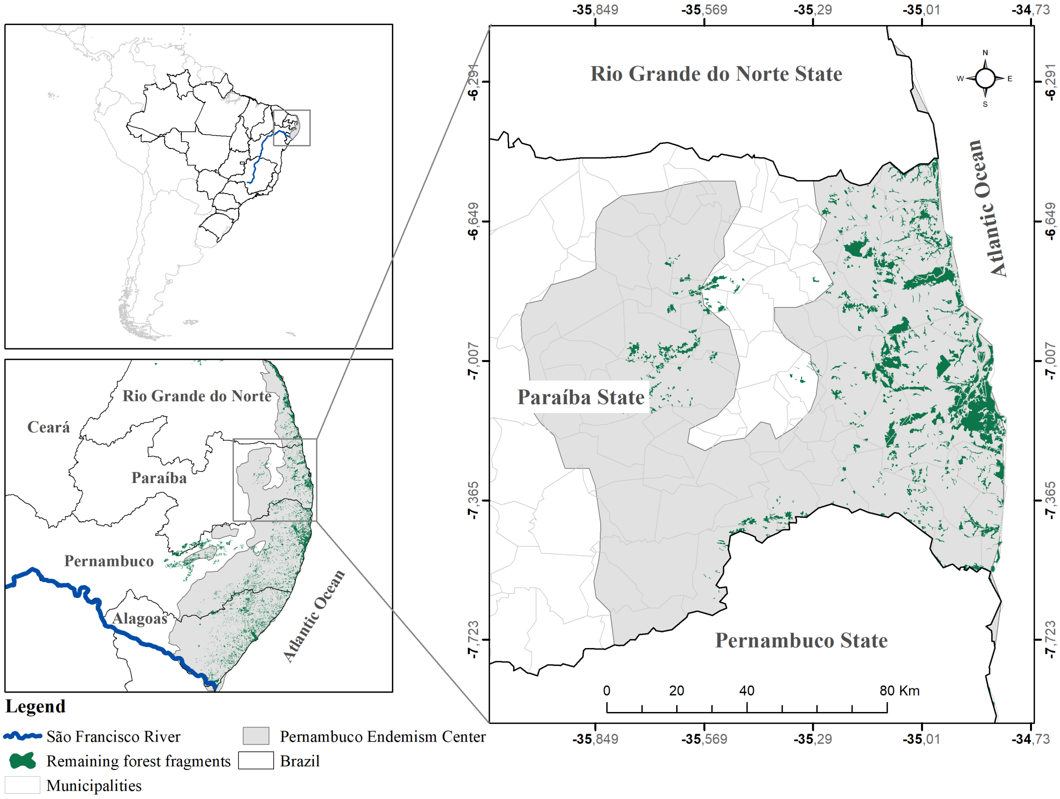

FIGURE 1
Map of the location of the Paraíba Atlantic Forest, with the original coverage of Atlantic Forest (gray), and the actual remnants (green).

Universidade Federal da Paraíba. Each threat factor was assigned a score ranging from 1 (indicating a lower risk) to 2–4 (indicating a higher risk) based on careful consideration and evaluation.

2.2.1 Distribution data

1. Distribution breadth (DB): It is a crucial factor in assessing the vulnerability of species to extinction. The underlying principle is that species with smaller home ranges are more susceptible to extinction due to limited population densities, which can impact their ability to persist and survive during times of crisis (Purvis et al., 2000; Primack and Rodrigues, 2001). To determine the distribution breadth, we compiled data from species records within the municipalities encompassed by the Paraíba Atlantic Forest. The scoring system used for distribution breadth classification was as follows: 1 = wide distribution (present in > 80% of the territory); 2 = less broad (present in 50–80%); 3 = moderately restricted (present in 20–50%); 4 = restricted (present in <20%). In this work, we estimate the distribution area of the species through the minimum convex polygon (MCP) method. The MCP is the most used estimator to calculate the home range of a species and is designed to be the smallest possible polygon that covers all the points of record of the species (Laver and Kelly, 2008).

2. Habitat breadth (HB): The underlying principle is that species with specialized habitat requirements are more susceptible to the impacts of human activities, as they may have limited ability to adapt to disturbances (Purvis et al., 2000; Primack and Rodrigues, 2001). This threat factor was motivated by the occurrence of species in five habitat types of the Paraíba Atlantic Forest (see Pereira-Filho et al., 2017): brejos nordestinos, stational semidecidual forest (closed forest), stational semidecidual forest (tabuleiros or savannahs), mangrove, and restinga. 1 = generalist (found in at least four categories); 2 = less generalist (found in three categories); 3 = moderate specialist (found in two categories); 4 = specialist (found in only one category).

3. Endemicity (E): It is based on the principle that endemic species with a more restricted distribution may be especially vulnerable to extinction (Andreone and Luiselli, 2000; Işik, 2011; Tomović et al., 2015). The categories are: 1 = 0–10% of the species' distribution occurs in the Paraíba Atlantic Forest; 2 = >10% of the species' distribution occurs in the Paraíba Atlantic Forest.

4. Rarity in the Paraíba Atlantic Forest (RR): The underlying principle is that small and isolated populations are more susceptible to extinction due to factors such as accelerated inbreeding, increased stochastic effects, and genetic drift, which can lead to a loss of genetic variability (Primack and Rodrigues, 2001; Piratelli and Francisco, 2013). Our rarity categories were created based on the percentage of the quantity of registered specimens (2625 records) in the Paraíba Atlantic Forest. 1 = > 8% of total recorded specimens; 2 = 6-8%; 3 = 2-6%; 4 = < 2%.

2.2.2 Ecological data

5. Dietary breadth (DT): It is based on the principle that species with a more specialist diet are more vulnerable to extinction due to the possibility of loss of prey or destruction of their prey's habitat caused by negative human interventions in their habitats (McKinney, 1997; Purvis et al., 2000; Boyles and Storm, 2007). The categories were created based on the level of taxonomic order of the prey and percentage of the main prey in the diet; 1 = generalist, main prey item < 30% of diet; 2 = low specialization, main prey 31–50% of diet; 3 = moderate specialization, main prey 51–70% of diet; 4 = highly specialized, main prey > 70% of diet.

6. Habitat use and activity period (HT): The underlying principle is that species with more secretive habits, such as fossorial (burrowing) and cryptozoic (cryptic or hidden) behavior, are generally less vulnerable to extinction. This is primarily because they are less likely to be detected by predators and less susceptible to direct harm from human activities (França and Araújo, 2006). 1 = fossorial species; 2 = species with nocturnal, cryptozoic, or aquatic activity; 3 = species with secretive diurnal activity; 4 = terrestrial species with diurnal activity.

7. Adaptability to altered environments (AH): The underlying principle is that species with greater adaptability to man-altered environments are generally less vulnerable to extinction, as they possess the ability to tolerate and persist in habitats that have been modified by human activities (Filippi and Luiselli, 2000). This category was based on the presence/absence of species in protected areas of the Paraíba Atlantic Forest: 1 = completely adapted (found even in urban environments); 2 = adapted (found in suburbs if there is natural environment nearby); 3 = less adapted (found in and near large natural environments); 4 = not adapted (found only within conservation units).

8. Direct anthropogenic effects on species conservation status (AE): The presence of direct anthropogenic effects can lead to a greater and faster reduction in the size of local populations, ultimately impacting their conservation status (Tomović et al., 2015). The categories were based on the presence of the following direct anthropogenic effects: roadkill (based on monitoring of road-killed snakes in the Paraíba Atlantic Forest (unpublished data; Pereira-Filho et al., 2017), consumption of snakes as human food, for medicinal, magic/religious, ornamental or decorative purposes, pets, target species of conflict (species that are commonly killed when in contact with humans) (Alves and Pereira-Filho, 2007; Pereira-Filho et al., 2017). The categories are: 1 = no effect; 2 = low effect (presence of one or two types of human impacts); 3 = medium effect (presence of three types of human impacts); 4 = high effect (presence of four or more types of human impacts) on the species.

2.2.3 Life-history data

9. Body size (BS): It is based on the principle that larger species tend to occur at lower densities, have larger home ranges, and reach sexual maturity later, making them more susceptible to negative human interventions in their habitats (McKinney, 1997; Purvis et al., 2000; Dulvy and Reynolds, 2002). The categories are: 1 = < 50 cm length; 2 = 51–100 cm length; 3 = 101–150 cm length; 4 = > 150 cm length.

10. Litter size (LS): Eggs or younglings; it is based on the principle that species with low fecundity are more vulnerable to extinction. This is because if such species experience a significant decrease in population size, it becomes more challenging for them to recover their original population levels (Purvis et al., 2000; Dulvy and Reynolds, 2002; Webb et al., 2002). The categories are: 1 = The maximum number of litters > 15; 2 = 11–15; 3 = 5–10; 4 = < 5.

11. Reproduction mode (RM): Viviparous species tend to produce fewer offspring than oviparous and are more prone to extinction risks (Andreone and Luiselli, 2000). The categories are: 1 = oviparity; 2 = viviparity.

12. Frequency of reproduction (FR): A taxon that can reproduce throughout the year can recuperate more easily when habitats are altered (Tomović et al., 2015; Vukov et al., 2015). The categories are: 1 = aseasonal reproduction; 2 = seasonal reproduction.

2.3 Statistical procedures

To determine the relative threat levels for each species of snake, the mean scores for the 12 threat factors mentioned above were calculated. Before computing the mean score, we standardized the scores for each variable, ranging them from zero to one. This standardization allows for a uniform comparison of the threat levels across different factors. Scores closer to 1 indicate higher risks of threat, while scores closer to zero indicate lower risks.

Next, we employed principal component analysis (PCA) and cluster analysis to assess how species are classified based on their similarity in terms of specific threats. The cluster analysis employed the UPGMA model, which generates an agglomerative hierarchical classification dendrogram. All analysis were conducted using the software R, version 3.2.0.

To evaluate the relative threat level for each snake species within the community, we followed the approach outlined by Tomović et al. (2015). We categorized the mean scores into five groups, based on the classification proposed by the IUCN. Specifically, 40% of the species with the lowest mean scores were considered Least Concern (LC, 0–40%). The remaining 60% of species were equally distributed among four categories of threatened species: near threatened (NT, 41–55%), vulnerable (VU, 56–70%), endangered (EN, 71–85%), and critically endangered (CR, 86–100%).

The results obtained in this study for the Paraíba Atlantic Forest snakes were compared with the results obtained by França and Araújo (2006) who evaluated the vulnerability to extinction of snakes in central Brazil using intrinsic and extrinsic factors. Additionally, we also compared our results with assessments conducted using the IUCN methodology and various regional red lists to examine if the same species exhibit similar degrees of vulnerability across different regions and methodologies. To assess the consistency of vulnerability levels, we referred to the red list of threatened species published by the IUCN (IUCN, 2022), the Brazilian red list of threatened species (MMA, 2022), and four regional lists: red list of threatened species of the Pernambuco state (SEMAS, 2017), red list of threatened species of the Bahia (SEMA, 2017), the Rio Grande do Sul state (Rio Grande do Sul, 2014), and of the Espírito Santo state (Vitória, 2022).

3 Results

3.1 Comparison of mean scores and threat factors

In Table 1 we present the scores for each species and each threat factor used to evaluate the vulnerability to extinction of the 55 snake species that were found in the Paraíba Atlantic Forest (more details see Supplementary Material, Table 1). The mean values of the scores for all species varied between 0.19 (lower risk) and 0.75 (higher risk). The categories, criteria, and amplitude of the scores for the five categories proposed by IUCN (LC, NT, VU, EN, CR) are presented in Table 2.

Our results indicate that only 10 species (18%) of snakes present no risk of decline, 24 species (44%) are considered near threatened, 9 (16%) are considered vulnerable, 9 (16%) species are considered endangered, and 3 species (5%) are considered critically endangered. *Helicops angulatus* and *Oxyrhopus trigeminus* had the lowest mean scores of 0.19 and 0.28 respectively, while *Caaeteboia gaeli* and *Crotalus durissus* presented the highest mean scores, 0.75 and 0.72, respectively.

Threat factors related to species distribution contributed more to the mean scores of 21 species (*Amerotyphlops arenensis*, *A. brongersmianus*, *Apostolepis cearensis*, *A. longicaudata*, *Boiruna sertaneja*, *Corallus hortulana*, *C. gaeli*, *Drymarchon corais*, *Erythrolamprus almadensis*, *E. miliaris*, *E. taeniogaster*, *Epictia*

TABLE 1 Values for the 12 threat factors that may affect the survival of snakes in the Paraíba Atlantic Forest.

	Distribution				Ecological data				Life-history data				
Família/Espécie	DB	HB	E	RR	DT	HT	AH	AE	BS	LS	RM	FR	Mean score
Boidae													
Boa constrictor	3	1	1	4	2	2	3	4	4	1	2	2	0.56
Corallus hortulana	4	3	1	4	3	2	4	2	2	1	2	2	0.61
Epicrates assisi	1	2	1	3	4	2	1	4	3	2	2	2	0.53
Colubridae													
Chironius exoletus	3	2	1	4	4	4	4	1	3	2	1	2	0.58
Chironius flavolineatus	2	2	1	3	4	3	2	1	3	3	1	2	0.47
Dendrophidion atlantica	4	4	1	4	4	4	4	1	2	4	1	1	0.61
Drymarchon corais	4	3	1	4	1	4	3	2	4	2	1	1	0.50
Drymoluber dichrous	3	2	1	4	4	4	3	1	2	3	1	1	0.47
Leptophis ahaetulla	3	3	1	4	4	4	2	2	3	2	1	1	0.50
Oxybelis aeneus	2	2	1	4	4	3	2	2	4	3	1	2	0.56
Palusophis bifossatus	4	3	1	4	4	4	3	1	4	1	1	2	0.61
Spilotes sulphureus	4	4	1	4	4	4	3	2	4	2	1	1	0.61
Spilotes pullatus	2	2	1	4	4	4	3	4	4	2	1	2	0.64
Tantilla melanocephala	2	1	1	3	4	1	4	2	1	4	1	1	0.36
Dipsadidae													
Apostolepis longicaudata	4	4	1	4	4	1	4	1	1	4	1	1	0.50
Apostolepis cearensis	4	3	1	4	4	1	3	1	2	4	1	1	0.47
Boiruna sertaneja	3	4	1	4	3	2	2	2	4	2	1	1	0.47
Caaeteboia gaeli	4	4	2	4	4	4	4	1	1	4	1	2	0.75
Erythrolamprus miliaris	4	4	1	4	4	2	4	1	3	1	1	1	0.50
Erythrolamprus almadensis	4	4	1	4	4	3	3	1	1	3	1	1	0.50
Erythrolamprus poecilogyrus	3	1	1	4	4	4	2	2	2	1	1	1	0.39
Erythrolamprus taeniogaster	4	3	1	4	3	3	3	1	2	3	1	1	0.47
Erythrolamprus viridis	3	4	1	4	4	4	2	2	1	3	1	1	0.50
Helicops angulatus	2	2	1	1	4	2	1	1	2	1	1	1	0.19

(Continued)

TABLE 1 Continued

	Distribution				Ecological data				Life-history data				
Família/Espécie	DB	HB	E	RR	DT	HT	AH	AE	BS	LS	RM	FR	Mean score
Hydrodynastes gigas	3	3	1	4	1	2	3	1	4	1	1	2	0.44
Imantodes cenchoa	4	3	1	4	4	2	3	2	3	3	1	1	0.53
Lygophis dilepis	3	3	1	4	4	4	2	2	1	3	1	1	0.47
Oxyrhopus guibei	3	2	1	4	4	2	4	1	2	1	1	1	0.39
Oxyrhopus petolarius	2	2	1	4	2	2	3	2	3	2	1	1	0.36
Oxyrhopus trigeminus	1	1	1	2	3	2	1	4	2	3	1	1	0.28
Philodryas nattereri	1	2	1	3	3	4	1	3	4	2	1	2	0.47
Philodryas olfersii	1	1	1	3	3	4	1	4	3	1	1	2	0.42
Pseudablabes patagoniensis	3	2	1	3	2	4	1	2	3	1	1	2	0.42
Phimophis guerini	3	2	1	4	4	2	3	2	2	3	1	1	0.44
Pseudoboa nigra	2	2	1	3	4	2	2	2	3	1	1	1	0.33
Psomophis joberti	4	4	1	4	2	4	2	1	1	3	1	2	0.53
Sibon nebulatus	4	3	1	4	4	2	3	2	2	3	1	2	0.58
Dipsas neuwiedi	3	3	1	4	4	2	3	2	1	2	1	2	0.50
Dipsas mikanii	1	2	1	3	4	2	2	2	1	3	1	2	0.39
Siphlophis compressus	4	4	1	4	4	2	3	2	2	2	1	2	0.58
Dibernardia affinis	4	2	1	4	2	2	4	1	1	3	1	2	0.47
Adelphostigma occipitalis	2	2	1	3	4	2	3	1	1	4	1	2	0.44
Thamnodynastes hypoconia	4	4	1	4	4	2	4	1	2	2	2	2	0.67
Thamnodynastes pallidus	4	3	1	3	4	2	4	2	2	3	2	2	0.67
Xenodon merremii	2	2	1	3	4	4	3	2	2	1	1	1	0.39
Xenopholis undulatus	4	4	1	4	4	2	4	1	1	4	1	2	0.61
Elapidae													
Micrurus ibiboboca	1	2	1	2	3	2	1	3	3	2	1	2	0.36
Micrurus potyguara	3	3	2	4	3	2	1	2	2	2	1	2	0.53
Leptotyphlopidae													
Epictia borapeliotes	4	3	1	4	4	1	3	1	1	2	1	2	0.47
Typhlopidae													
Amerotyphlops arenensis	4	4	2	4	4	1	4	1	1	3	1	2	0.64
Amerotyphlops brongersmianus	4	3	1	3	4	1	4	1	1	3	1	2	0.50
Amerotyphlops paucisquamus	4	3	1	1	4	1	4	1	1	4	1	2	0.47
Viperidae													
Bothrops leucurus	1	2	1	3	2	2	2	2	4	1	2	2	0.44
Crotalus durissus	4	4	1	4	4	2	3	4	3	1	2	2	0.72
Lachesis muta	4	4	1	4	4	2	4	3	4	2	1	2	0.69

DB, Distribution breadth; HB, Habitat breadth; E, Endemicity; RR, Rarity in the Paraíba Atlantic Forest; DT, Dietary breadth; HT, Habitat use and activity period; AH, Adaptability to altered environments; AT, Direct anthropogenic effects on species conservation status; BS, Body size; LS, Litter size; RM, Reproduction mode; FR, Frequency of reproduction.

TABLE 2 Categories, criteria and score ranges for species of snakes of the Atlantic Forest of Paraíba.

Category	Criteria	Range
LC	Lowest 40% of score range of complete assemblage	0.19-0.41
NT	41–55% of score range of complete assemblage	0.42-0.50
VU	56–70% of score range of complete assemblage	0.51-0.58
EN	71–85% of score range of complete assemblage	0.59-0.67
CR	85-100% of score range of complete assemblage	0.68-0.75

borapeliotes, *Hydrodynastes gigas*, *Imantodes cenchoa*, *Micrurus potyguara*, *Psomophis joberti*, *Siphlophis compressus*, *Sibon nebulatus*, *Dibernardia affinis*, *Thamnodynastes hypoconia*, and *Xenopholis undulatus*). The factors related to ecology played a more prominent role in determining to the mean scores of 15 species (*Chironius exoletus*, *Drymoluber dichrous*, *Dipsas mikanii*, *Erythrolamprus poecilogyrus*, *H. angulatus*, *Leptophis ahaetulla*, *Lygophis dilepis*, *Oxyrhopus guibei*, *O. trigeminus*, *Phimophis guerini*, *Pseudoboa nigra*, *Philodryas olfersii*, *Spilotes pullatus*, *Tantilla melanocephala*, and *Xenodon merremii*), and the factors related to natural history contributed more to the mean scores of 7 species (*Boa constrictor*, *Bothrops leucurus*, *Chironius flavolineatus*, *Epicrates assisi*, *Micrurus ibiboboca*, *Oxybelis aeneus*, and *Thamnodynastes pallidus*). For 8 species (*C. durissus*, *Dendrophidion atlantica*, *Dipsas neuwiedi*, *Erythrolamprus viridis*, *Lachesis muta*, *Palusophis bifossatus*, *Oxyrhopus petolarius*, and *Spilotes sulphureus*), factors related to both distribution and ecology were the main contributors to the mean scores, while for three species (*Amerotyphlops paucisquamus*, *Philodryas nattereri*, and *Adelphostigma occipitalis*), factors related to both ecology and natural history were the main contributors, and for only one species (*Pseudablabes patagoniensis*), all factors contributed in the same way (Figure 2).

3.2 Principal component analysis and cluster analysis

We used PCA to classify the snake species that occur in the Paraíba Atlantic Forest into groups of threat to specific factors; however, these groups are not easily visualized in the graph of the analysis (Figure 3), and so it was combined with the cluster analysis.

The values of the variables for the first three main components are presented in Table 3. The first two axes explained 49% of the variation in the data. The variables most significantly associated with the main component 1 were the direct anthropogenic effects on species conservation status, which was negatively related, and the adaptability to altered environments and distribution breadth, which were positively related. The variables most significantly associated with the main component 2 were frequency of reproduction and reproduction mode, both positively related.

We used PCA and cluster analysis to distinguish 10 groups of snake species in the Paraíba Atlantic Forest (Figure 4). Of these, two groups were considered non-threatened and five groups were considered threatened. All natural history information, distribution, and other threat factors refer to the data obtained for PAF snakes. The groups are described below.

Group 1= Non-endemic species, with large body size, produce large numbers of offspring, oviparous, and with seasonal reproduction (Non-threatened and Threatened): *M. ibiboboca*, *P. nattereri*, *P. olfersii*, *P. patagoniensis*, and *S. pullatus*.

Group 2= Non-endemic species, rare in PAF, with a large body size, produce large numbers of offspring, viviparous, and with seasonal reproduction (Threatened): *B. constrictor*, *B. leucurus*, and *E. assisi*.

Group 3= Species with wide distribution, non-endemic, adapted to altered environments, with aseasonal reproduction, and oviparous (Not Threatened): *H. angulatus* and *O. trigeminus*.

Group 4= Non-endemic species, adapted to altered environments, oviparous, and with seasonal reproduction (Non-threatened and threatened): *A. brongersmianus*, *A. paucisquamus*, *C. flavolineatus*, *D. mikanii*, *D. neuwiedi*, *E. borapeliotes*, *O. aeneus*, *P. joberti*, *S. nebulatus*, *S. compressus*, *D. affinis*, *A. occipitalis* and *X. undulatus*.

Group 5= Non-endemic species, rare in PAF, with a large body size, produce large numbers of offspring, oviparous, and

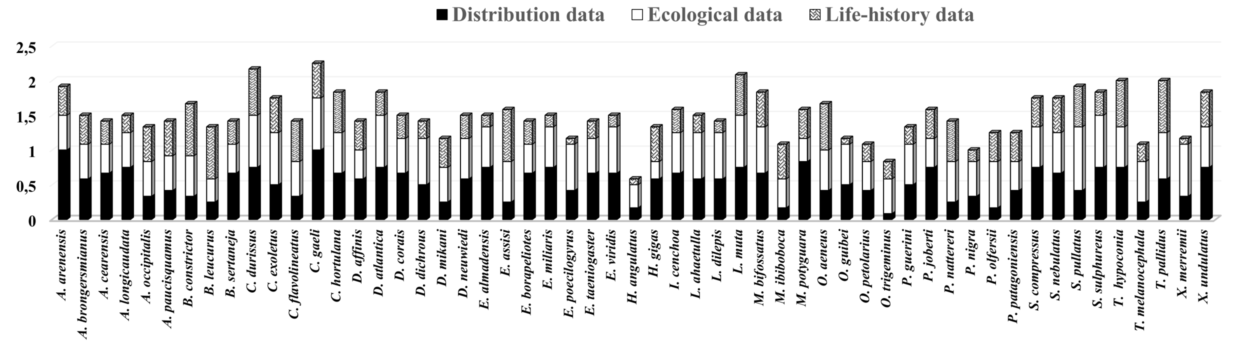

FIGURE 2
Mean scores for the distribution, ecology, and life-history data contributing to extinction risk of the Paraíba Atlantic Forest Snakes.

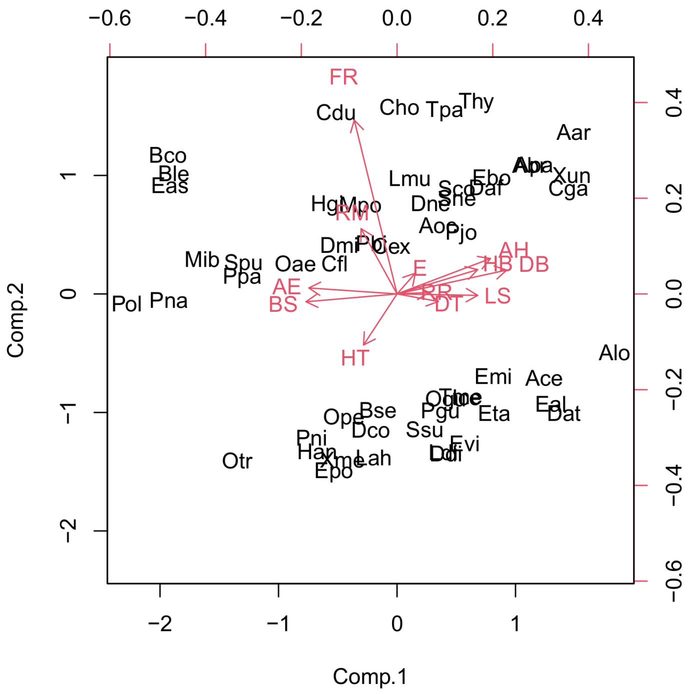

FIGURE 3
Scores of threat factors for the main components of the snake species of the Paraíba Atlantic Forest, showing some threatened groups. Aar, *Amerotyphlops arenensis*; Abr, *Amerotyphlops brongersmianus*; Ace, *Apostolepis cearensis*; Alo, *Apostolepis longicaudata*; Apa, *Amerotyphlops paucisquamus*; Bco, *Boa constrictor*; Ble, *Bothrops leucurus*; Bse, *Boiruna sertaneja*; Cdu, *Crotalus durissus*; Cex, *Chironius exoletus*; Cfl, *Chironius flavolineatus*; Cho, *Corallus hortulana*; Cga, *Caaeteboia gaeli*; Dat, *Dendrophidion atlantica*; Dco, *Drymarchon corais*; Ddi, *Drymoluber dichrous*; Dmi, *Dipsas mikanii*; Dne, *Dipsas neuwiedi*; Eal, *Erythrolamprus almadensis*; Eas, *Epicrates assisi*; Ebo, *Epictia borapeliotes*; Emi, *Erythrolamprus miliaris*; Epo, *Erythrolamprus poecilogyrus*; Eta, *Erythrolamprus taeniogaster*; Evi, *Erythrolamprus viridis*; Han, *Helicops angulatus*; Hgi, *Hydrodynastes gigas*; Ice, *Imantodes cenchoa*; Lah, *Leptophis ahaetulla*; Ldi, *Lygophis dilepis*; Lmu, *Lachesis muta*; Pbi, *Palusophis bifossatus*; Mib, *Micrurus ibiboboca*; Mpo, *Micrurus potyguara*; Oae, *Oxybelis aeneus*; Ogu, *Oxyrhopus guibei*; Ope, *Oxyrhopus petolarius*; Otr, *Oxyrhopus trigeminus*; Pgu, *Phimophis guerini*; Pjo, *Psomophis joberti*; Pna, *Philodryas nattereri*; Pni, *Pseudoboa nigra*; Pol, *Philodryas olfersii*; Ppa, *Pseudablabes patagoniensis*; Sco, *Siphlophis compressus*; Sne, *Sibon nebulatus*; Spu, *Spilotes pullatus*; Ssu, *Spilotes sulphureus*; Daf, *Dibernardia affinis*; Thy, *Thamnodynastes hypoconia*; Tme, *Tantilla melanocephala*; Aoc, *Adelphostigma occipitalis*; Tpa, *Thamnodynastes pallidus*; Xme, *Xenodon merremii*; Xun, *Xenopholis undulates*.

with seasonal reproduction (Threatened): *C. exoletus*, *H. gigas*, *L. muta* and *P. bifossatus*.

Group 6= Species with restricted distribution, non-endemic, rare in PAF, with specialist diet, viviparous, and with seasonal reproduction (Threatened): *C. hortulana*, *C. durissus*, *T. hypoconia* and *T. pallidus*.

Group 7= Non-endemic species, rare in PAF, oviparous, and with aseasonal reproduction (Non-threatened and Threatened): *A. cearensis*, *A. longicaudata*, *B. sertaneja*, *D. atlantica*, *D. corais*, *D. dichrous*, *E. almadensis*, *E. miliaris*, *E. poecilogyrus*, *E. taeniogaster*, *E. viridis*, *I. cenchoa*, *L. ahaetulla*, *L. dilepis*, *O. guibei*, *O. petolarius*, *P. guerini*, *P. nigra*, *S. sulphureus* and *X. merremii*.

Group 8= Non-endemic species, generalists in habitat use, with a small body size, specialist diet, produce small numbers of offspring, oviparous, and with aseasonal reproduction (Not Threatened): *T. melanocephala*.

Group 9= Species with restricted distribution in PAF, endemic, rare in PAF, with specialist diet, and not adapted to altered environments (Threatened): *A. arenensis* and *C. gaeli*.

Group 10= Endemic species, rare in PAF, adapted to altered environments, oviparous, and with seasonal reproduction (Threatened): *M. potyguara*.

3.3 Vulnerability to extinction: comparison with pre-existing assessments

Among the 55 snake species found in the PAF, 23 species also occur in Central Brazil, where the Cerrado Biome is present (Table 4). The species *E. poecilogyrus* and *X. merremii* were considered least concern in both localities, whereas *B. constrictor* was deemed vulnerable in both regions. The species *C. exoletus* and *O. aeneus*, considered as vulnerable in the PAF, were considered threatened for Central Brazil. *C. durissus* considered critically endangered in PAF, was considered vulnerable for Central Brazil. The species *P. bifossatus*, *S. pullatus* and *T. hypoconia* considered as endangered in PAF, were considered as vulnerable for Central Brazil and the species *X. undulatus*, considered endangered in PAF, was considered threatened for Central Brazil (Table 4).

TABLE 3 Factor loadings of each variable on the first three principal components before VARIMAX rotation and proportion of the variance explained by each component.

Variable	Factor I	Factor II	Factor III
Distribution breadth in Atlantic Forest of Paraíba	0.8031354	0.17495013	0.46784739
Habitat breadth	0.6598637	0.19926977	0.44613306
Endemicity	0.2103440	0.23859863	-0.07072313
Rarity in the Paraíba Atlantic Forest	0.3398277	0.01613331	0.62817297
Dietary breadth	0.3918028	-0.07125953	-0.24809935
Habitat use and activity period	-0.2478528	-0.37790366	0.41896548
Adaptability to altered environments	0.7203346	0.27296783	0.22664127
Direct anthropogenic effects on species conservation status	-0.7333963	0.04985458	0.01165817
Body size	-0.6506860	-0.05582365	0.58094806
Litter size	0.6240426	-0.01081804	-0.48146304
Reproduction mode	-0.2817180	0.51125202	0.20777356
Frequency of reproduction	-0.2264930	0.92081468	-0.07181117
% Variance	0.2874514	0.2017763	0.1340658
% Cumulative variance	0.2874514	0.4892277	0.6232935

In reference to the IUCN list of threatened species, *M. potyguara* was listed as near threatened and *D. atlantica* as data deficient. Two species (*A. arenensis* and *C. gaeli*), have yet to be evaluated. The remaining species on the list were considered of least concern, implying a lower risk of extinction. It's worth noting that none of the 55 snake species from the PAF are currently listed on the Brazilian threatened species list.

When comparing the regional red lists of threatened species from Pernambuco, Bahia, Rio Grande do Sul, and Espírito Santo states with the vulnerability assessments conducted in the PAF, interesting patterns emerge. The red list from Pernambuco state, which is a neighboring state to Paraíba, showed the highest similarity in terms of the degree of vulnerability of snake species. The species *E. poecilogyrus*, *H. angulatus*, *O. guibei*, *O. petolarius*, *O. trigeminus*, *P. nigra*, *T. melanocephala*, and *X. merremii* were considered as least concern both for the state of Pernambuco and for PAF, while *S. compressus* was considered vulnerable in both states. The species *B. constrictor*, *C. exoletus*, *E. assisi*, *I. cenchoa*, and *O. aeneus*, considered vulnerable, the species *C. hortulana*, *T. pallidus*, *S. pullatus* and *P. bifossatus* considered endangered, and *C. durissus*, considered critically endangered at the PAF, were considered of least concern to the Pernambuco state.

The species *H. gigas* was classified as vulnerable in the state of Rio Grande do Sul but considered near threatened in the PAF. While the species *X. undulatus*, considered threatened in Central Brazil and listed as data deficient (DD) for the state of Pernambuco, was considered endangered in the PAF. Furthermore, *L. muta*, which is vulnerable in the state of Pernambuco, and Bahia, was considered critically endangered in the state of Espírito Santo and in the present study. Although the faunas of Rio Grande do Sul, Bahia, and Espírito Santo states share few similar species with PAF, some species of the genus *Corallus*, *Apostolepis*, *Philodryas*, and *Bothops* that were considered threatened in the PAF were also considered threatened in these other lists.

4 Discussion

Filippi and Luiselli (2000) proposed that factors associated with geographic distribution were the most important threats to the Italian snake fauna; however, factors related to the natural history of the species could also be influencing the viability of some species. For the Cerrado of Central Brazil França and Araújo (2006), found that both factors related to geographic distribution and natural history could affect the viability of snake populations. In contrast, the study conducted on Serbian snakes by Tomović et al. (2015) found that factors related to the natural history of the species contributed more to the conservation scores of the species. Regarding the PAF snakes and the study by Filippi and Luiselli (2000), the results indicate that factors related to species distribution (1–4) contribute more to the threat scores of snake species.

Our findings highlight several factors that contribute to the vulnerability of snake species in the Atlantic Forest, particularly in the Paraíba region. These factors include restricted distribution, rarity, and specialized diets, all of which increase the susceptibility of species to threats and population decline. Over the years, forest cover in the Paraíba region has been drastically reduced due mainly to the expansion of sugarcane cultivation and the development of activities related to shrimp farming in mangrove areas (Tabarelli et al., 2006). Currently, only small fragments remain on private property and some protected areas designated by the government (Barbosa et al., 2004). Unfortunately, these fragmented habitats are often insufficient to support the survival of many animal populations, including snakes. Thus, even species that present a very wide distribution, such as *L. muta*, which occurs throughout half of the Atlantic Forest and the Amazon, but only in large and well-preserved areas (Dixon and Soini, 1986; Marques et al., 2004), could become locally or regionally extinct in the PAF.

Numerous studies have demonstrated that snake species with specialized diets are more susceptible to extinction compared to generalists. This increased vulnerability stems from the potential loss of prey species or the destruction of their prey's habitats, which directly impact the survival and reproductive success of these specialized snakes (Boyles and Storm, 2007). The significance of the diet factor in assessing the threat levels of snake species has been observed in various regions, including the PAF, the Cerrado of Central Brazil, and Italian snake populations. In these different contexts, studies such as França and Araújo (2006) and Filippi and Luiselli (2000) have consistently shown high vulnerability values associated with the diet factor, underscoring the importance of careful analysis and consideration of this factor in evaluating the conservation status of snake species.

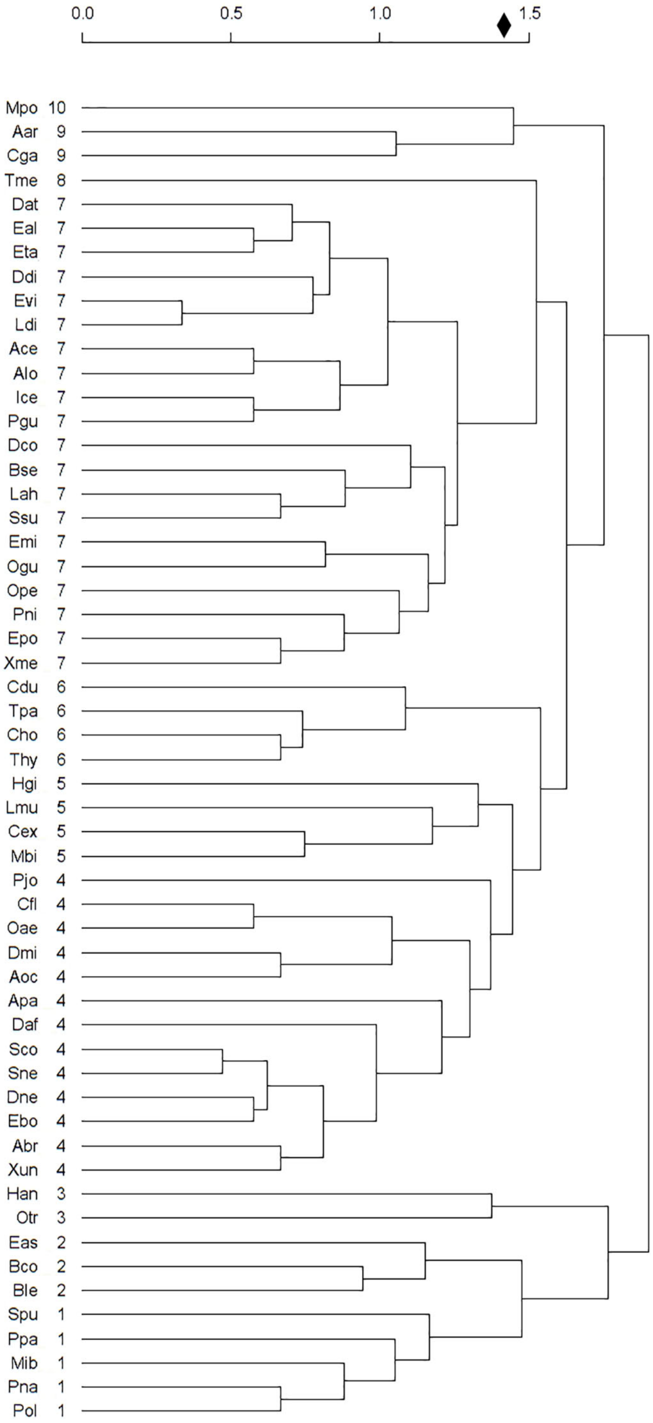

FIGURE 4
Cluster diagram showing the similarity groups for threatening factors among fifty-five snake species of Paraíba Atlantic Forest. Diamond indicates the point in cluster diagram where significance is achieved. Numbers to the right of species indicate the groups. The abbreviations are the same as those used in Figure 3.

When comparing the species groups formed through PCA in our present study with those of França and Araújo (2006), we identified both similarities and differences among certain groups. The species of the Boidae family are vulnerable or threatened in PAF and Cerrado, due mainly to their large size and by being significantly affected by direct anthropogenic effects, whereas contradictory results were observed among the Viperidae family. The viperids found in PAF were mainly threatened due to small population sizes and rarity, while in the Cerrado most species of this family exhibit wider distribution ranges and larger population sizes, reflecting low vulnerability levels.

Of the 23 species found in both the Atlantic Forest of Paraíba and the Cerrado (França and Araújo, 2006), the species *E.*

TABLE 4 Comparison between the degree of vulnerability to extinction of the snakes species of the Paraíba Atlantic Forest with preexisting assessments: International Union for Conservation of Nature (IUCN, 2022-2), Central Brazil (França and Araújo, 2006); Pernambuco state (PE) (SEMAS, 2017); Bahia (BA) (SEMA, 2017); Rio Grande do Sul state (RS) (Rio Grande do Sul, 2014) and Espírito Santo state (ES) (Vitória, 2022).

Species	IUCN	PAF	PE	BA	RS	ES	Central Brazil
Amerotyphlops arenensis		EN					
Amerotyphlops brongersmianus	LC	NT	LC				
Amerotyphlops paucisquamus	LC	NT	LC				
Apostolepis cearensis	LC	NT	LC				
Apostolepis longicaudata	LC	NT	DD			CR	
Boa constrictor	LC	VU	LC				VU
Boiruna sertaneja	LC	NT	LC				
Bothrops leucurus	LC	NT	LC				
Caaeteboia gaeli		CR					
Chironius exoletus	LC	VU	LC				Th
Chironius flavolineatus	LC	NT	LC				VU
Corallus hortulana	LC	EN	LC				
Crotalus durissus	LC	CR	LC				VU
Dendrophidion atlantica	DD	EN	DD				
Dipsas mikanii	LC	LC					
Dipsas neuwiedi	LC	NT	LC				VU
Drymarchon corais	LC	NT	LC				VU
Drymoluber dichrous	LC	NT	VU				
Epicrates assisi	LC	VU	LC				
Epictia borapeliotes	LC	NT	LC				
Erythrolamprus almadensis	LC	NT	LC				Th
Erythrolamprus miliaris	LC	NT	LC				
Erythrolamprus poecilogyrus	LC	LC	LC				no risk
Erythrolamprus taeniogaster	LC	NT	LC				
Erythrolamprus viridis	LC	NT	LC				
Helicops angulatus	LC	LC	LC				Th
Hydrodynastes gigas	LC	NT			VU		
Imantodes cenchoa	LC	VU	LC				
Lachesis muta	LC	CR	VU	VU		CR	
Leptophis ahaetulla	LC	NT	LC				
Lygophis dilepis	LC	NT	LC				
Micrurus ibiboboca	DD	LC	DD				
Micrurus potyguara	NT	VU	DD				
Oxybelis aeneus	LC	VU	LC				Th
Oxyrhopus guibei	LC	LC	LC				VU
Oxyrhopus petolarius	LC	LC	LC				
Oxyrhopus trigeminus	LC	LC	LC				Th
Palusophis bifossatus	LC	EN	LC				VU

(Continued)

TABLE 4 Continued

Species	IUCN	PAF	PE	BA	RS	ES	Central Brazil
Philodryas nattereri	LC	NT	LC				no risk
Philodryas olfersii	LC	NT	LC				no risk
Pseudablabes patagoniensis	LC	NT	LC				no risk
Phimophis guerini	LC	NT					Th
Pseudoboa nigra	LC	LC	LC				Th
Psomophis joberti	LC	VU					
Sibon nebulatus	LC	VU					
Siphlophis compressus	LC	VU	VU				
Spilotes pullatus	LC	EN	LC				VU
Spilotes sulphureus	LC	EN					
Dibernardia affinis	LC	NT					
Adelphostigma occipitalis	LC	NT	LC				
Tantilla melanocephala	LC	LC	LC				VU
Thamnodynastes hypoconia	LC	EN	DD				VU
Thamnodynastes pallidus	LC	EN	LC				
Xenodon merremii	LC	LC	LC				no risk
Xenopholis undulatus	LC	EN	DD				Th

DD, Data Deficient; LC, least concern; NT, Near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; Th, Threatened.

poecilogyrus, *X. merremii*, and *B. constrictor* showed similar results in their degree of vulnerability. In addition, some other species (*C. exoletus*, *C. durissus*, *P. bifossatus*, *S. pullatus*, *T. hypoconia*, and *X. undulatus*) were identified as threatened in both the Atlantic Forest and the Cerrado, albeit at varying levels. This suggests that some species are subject to similar threats even in different biomes. For instance, *C. exoletus* and *X. undulatus* are rare species, with restricted distributions, and low adaptability to live in altered environments in both regions, while the conservation status of the species *C. durissus* is greatly affected by direct anthropogenic effects in both regions. The comparison of species conservation statuses in distinct habitats, using different methodologies that yield similar results, highlights the importance of assessing species vulnerability across different biomes. This comparative analysis underscores the need for careful evaluation and conservation considerations for species that exhibit consistent degrees of vulnerability in diverse habitats. Such species may be particularly susceptible to threats and require targeted conservation efforts to ensure their long-term survival.

Caaeteboia gaeli, a recently described species, exhibited the highest vulnerability index in the Paraíba Atlantic Forest, classifying it as critically endangered with a vulnerability index of 0.75. The species is known from only three specimens, with two individuals found in the Atlantic Forest of Paraíba and one in the state of Pernambuco (Montingelli et al., 2020). Prior to the description of *C. gaeli*, the only known species in the genus was *C. amarali*, which has a known distribution in the states of Bahia, Minas Gerais, São Paulo, Paraná, and Santa Catarina (Passos et al., 2012). *C. amarali* is sparsely represented in herpetological collections, with fewer than 15 specimens recorded until 2012 (Passos et al., 2012). In the red list of threatened species, this snake was considered endangered in the state of Bahia (SEMA, 2017), vulnerable in São Paulo (Marques et al., 2009), and data deficient in Paraná (Mikich and Bérnils, 2004). In our study, *C. gaeli* was considered threatened, mainly because of its rarity (only 3 known specimens), specialized in habitat and diet, and has not been found in altered environments. Consistent with Marques et al. (2009), the main threats to *C. amarali* in São Paulo state arise from habitat destruction and alteration caused by urbanization, housing development, and tourism along the coastal areas.

Our study findings reveal that the species *C. durissus* is critically endangered in the PAF (vulnerability index 0.72), mainly because it has a restricted distribution in PAF, is a specialist in habitat and diet, and is greatly affected by direct anthropogenic effects. Although the species has a wide distribution in Brazil (Boldrini-França et al., 2010), in PAF, this species was only found at a few localities (França et al., 2012; Mesquita et al., 2018). Besides the rarity, this species is threatened by anthropic use Notably, the skin and rattle of *C. durissus* have been associated with magical and religious rituals, particularly within Afro-Brazilian religions (Alves et al., 2012). Products such as rattlesnake rattles are frequently found in markets or specialty stores catering to mystical religious articles, primarily sought after by followers of Afro-Brazilian cults (Pereira-Filho et al., 2017). Furthermore, various parts of the snake's body, including the skin, tail, cloaca, rattle, and fat, are used in traditional folk medicine for treating ailments such as asthma, thrombosis, rheumatism, skin diseases, tuberculosis, hanseniasis, and osteoporosis (Alves et al., 2009). Regrettably, the use of *C. durissus* for ornamental and decorative purposes has also been documented in the state of Paraíba. For instance, some hunters utilize rattlesnakes in the production of keyrings, and their skin is employed in the manufacturing of belts (Mendonça et al., 2014).

The species *T. hypoconia* also had a high vulnerability index in the PAF (0.67), being considered endangered in the region, mainly because it has a restricted distribution and is rare in the PAF, is a habitat and diet specialist, and has low adaptability to living in altered environments. In Brazil, this species is distributed in the Atlantic Forest (Marques et al., 2004; França et al., 2020), Cerrado (Marques et al., 2015), and Caatinga (Guedes et al., 2014) biomes. In Paraíba, this species is quite common in the Caatinga Biome, but is rare within the PAF, with only two recorded specimens found in a specific region called Brejo de Altitude Paraíba (Pereira-Filho et al., 2017; França et al., 2020). Furthermore, displays a specialized diet, primarily feeding on anurans (Bellini et al., 2013), which further increases its vulnerability to extinction.

Another species that presented a high vulnerability index (0.69) is *L. muta*. Historically, this species was classified into two subspecies: *L. muta muta* (Linnaeus, 1766) and *L. muta rhombeata* (Wied-Neuwied, 1824). The former was primarily found in the Amazon Forest, while the latter had a distribution range extending from northern Rio de Janeiro to Paraíba, with some isolated populations potentially present in moist enclaves of Ceará and Piauí (Cardoso et al., 2003). The subspecies *L. muta rhombeata* appeared in several state red lists, being considered vulnerable for the state of Espírito Santo, endangered for Rio de Janeiro, and critically endangered for Minas Gerais (Martins and Molina, 2008). In a review of the genus, Fernandes et al. (2004) considered the two names to be synonyms of *L. muta*, and as a result, excluded the species from the IUCN red list (IUCN, 2012). However, the populations identified in the Atlantic Forest should still be considered threatened due to the great deterioration of this Biome (Campbell and Lamar, 2004). The lack of comprehensive ecological data for *L. muta*, coupled with the challenge of encountering individuals in the field or scientific collections, underscores its rarity and the difficulties associated with studying this species (Lira-da-silva et al., 2009). However, recent studies utilizing telemetry on resident and translocated individuals in southern Bahia have provided new insights into the habitat preferences of *L. muta*. Contrary to previous assumptions, these findings suggest that *L. muta* may exhibit a greater level of tolerance towards agroforestry regions and areas undergoing early regeneration, rather than being solely reliant on well-preserved forests (Padrón et al., 2022).

The species *X. undulatus*, with only two specimens registered for PAF obtained a high vulnerability index (0.61). In the Cerrado (França and Araújo, 2006), this species also appeared as threatened, while in the list of species of the state of São Paulo (Marques et al., 2009), it appeared as being vulnerable. The main threat for this species indicated by Marques et al. (2009) is destruction of their habitat.

As with the rattlesnake, *C. durissus* (CR), other snakes, such as *S. pullatus* (EN), *B. constrictor* (VU), and *E. assisi* (VU), also had their vulnerability to extinction index greatly influenced by direct anthropogenic effects, such as roadkill, consumption as a human food, and use of the species for medicinal, magic/religious, ornamental, or decorative purposes. These factors need attention due to their uniqueness and growth in the last decades (Pereira-Filho et al., 2017).

The impact of roadkill on wild animal species has gained significant attention from researchers worldwide (Trombulak and Frissell, 2000). In Brazil, several studies have addressed this issue, revealing the common occurrence of road-killed snakes (Turci and Bernarde, 2009; Santos et al., 2012). In addition, studies show the existence of the practice of intentional roadkill, and explain that people generally try to kill snakes, especially for the belief that they are dangerous and pose a threat to human life (Secco et al., 2014). Even in species that present periods of nocturnal activities where car traffic would be less intense, such as *E. assisi*, *O. trigeminus*, and *M. potyguara*, the rate of road-killed animals is high on roads in the state of Paraíba. This threat factor, as well as others used here, are not included in the IUCN criteria for extinction risk assessments (IUCN, 2022-2) and their inclusion deserves to be assessed.

One of the primary objectives of conservation biology is to gain insight into the ecological mechanisms that contribute to the vulnerability of certain species and their decline (Caughley, 1994). By understanding these mechanisms, researchers can anticipate the potential for species extinction, thereby enhancing the chances of their survival. In general, the snakes of the Paraíba Atlantic Forest have restricted distribution, are rare and show diet specialization. Our results indicate that only 18% of snake species in the Paraíba Atlantic Forest have no risk of declining and revealed some patterns that can help to direct the conservation efforts for this fauna. We understand the importance of the formal IUCN system for assessing the risk of species extinction. Here, we are simply suggesting the parallel use of alternative parameters (e.g., data related to natural history and species ecology) to assess species' vulnerability to extinction and define conservation priorities. This type of approach becomes necessary in situations where, for example, species population data is not available. It is worth noting that some species with high vulnerability indices in our study are not currently included in pre-existing red lists. This disparity highlights the importance of our research in identifying species that may have been overlooked or inadequately evaluated. Among these species are *B. constrictor*, *C. exoletus*, *C. durissus*, *S. pullatus*, and *T. hypoconia*, which appear as "least concern" or "data deficient" in the existing lists of threatened species. It is crucial to recognize that these species, despite their current classification, warrant further careful evaluation in future assessments.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

RF: Writing – original draft, Writing – review & editing, Formal analysis, Conceptualization, Data curation, Project administration. MS: Writing – review & editing, Supervision, Conceptualization, Resources. FF: Writing – review & editing, Supervision, Conceptualization, Data curation, Resources.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1301717/full#supplementary-material

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Community perspectives of flagship species: can conservation motivators mitigate human-wildlife conflict?

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Public perception of endangered species is crucial for successful management of community-based conservation and sustainability of national parks. By the method of choice experiment, our study evaluated conservation preferences and willingness to donate money for flagship and non-flagship species using a choice experiment with 409 residents living near the Lanstang river source of Sanjiangyuan National Park, China. We found that flagship species such as the Snow leopard (*Pristine plateau*) and White-lipped deer (*Przewalskium albirostris*) generated more conservation funds than non-flagship species. However, not all flagship species were accepted. Respondents disliked Tibetan brown bears (*Ursus arctos pruinosus*) due to direct human-wildlife conflicts such as bodily injury and property damage. Heterogeneity of preference was influenced by household income, religious beliefs, ethnicity, culture, and conservation awareness. Results can be used to establish a local community-participative framework by combining conservation motivations that alleviate human-wildlife conflict.

KEYWORDS

community-based conservation, national parks, conservancy motivations, flagship species, human-wildlife conflicts, choice experiment

1 Introduction

Protected areas are the keystone of global biodiversity conservation, a baseline for the typical earth ecosystem, endangered species, and maintenance of natural and cultural heritage (Schulze et al., 2018). The Chinese government developed a new, three-part classification system of protected areas by designating: 1) national parks (the main body); 2) nature reserves (intermediate); and 3) natural parks such as forest parks, wetland park, scenic areas, geo-parks, etc. (Supplementary). China decided to adopt the national park system in 2013, more than 150 years after the establishment of Yellowstone, the world's first national park (Mi et al., 2023). However, the concepts and goals of national parks in China and the U.S. are similar: 1) protection, defined as – " a particularly large geographical area of national importance, including intact ecosystems as well as important habitats for wildlife and plant species."And 2) harmony between people and nature to achieve sustainable management of natural resources, defined as – "a complex natural-ecological and socio-cultural system in which humans are an integral part" (Charles, 2021).

At 15th Conference of the Parties to the Convention on Biological Diversity in 2021, China formally established its first set of five national parks. Among them Sanjiangyuan National Park (SNP) is the biggest and covers nearly 2% of the total land area of China (Figure 1). SNP contains typical, but important aspects of the Qinghai-Tibet Plateau ecosystem which is extremely fragile due to the impacts of climate change and human activity (Di et al., 2017). SNP covers 5 counties, 15 towns and 68 administrative villages. More than 95% of the residents are Tibetans, making it a challenge to ensure the livelihoods of locals while preserving ecosystem integrity (Zhang et al., 2020). The Chinese government has implemented an Ecological Relocation Program for relocating some local people to new villages outside the park boundaries to reduce environmental impacts (Peng et al., 2020). However, such projects are expensive and many people, especially long-dwelling residents do not want to leave. SNP proposed and enacted "one household, one post" program in 2016. If one member of the household is employed as an ecological conservator; the whole family can join. Until now, nearly 20,000 herdsmen have been hired, increasing the average annual income of each household by 21,600 RMB (Zhao et al., 2018). This policy not only raises the living standard of herdsmen, but also increases their awareness of conservation by participating in conservation work (Zhao et al., 2018).

Community involvement in national park management has a good foundation in China due to its rich history of co-management experiences for nature reserves over the years (Zhang and Yang, 2020). Resource sustainability, human well-being, and conflict resolution of community-based conservation (CBC) are aligned with the goals of national parks in China (Lee, 2018). CBC approaches integrate multi-disciplinary fields such as political ecology, conservation psychology and environmental history to address social-ecological coupled system (Berkes, 2003; Galvin et al., 2018). Success depends on cooperation among many stakeholders, including collective villager groups, park authorities, government administrative units, NGOs (Non-Governmental Organizations), and other institutions (Berkes, 2007; Doak et al., 2014). In China, CBC policy should focus on community empowerment, supporting autonomy, adaptive co-management projects, equal distribution of benefits, the use of traditional ecological knowledge, and development of cultural-linked conservation ethic, but the social psychological factors are not receiving enough attention (He et al., 2020). For example, establishing a belief system and providing incentives for people to participate in conservation work are poorly developed (Trudgill, 2001; DeCaro and Stokes, 2008).

Residents living near SNP are influenced heavily by Tibetan Buddhism which follows the basic principles of kindheartedness,

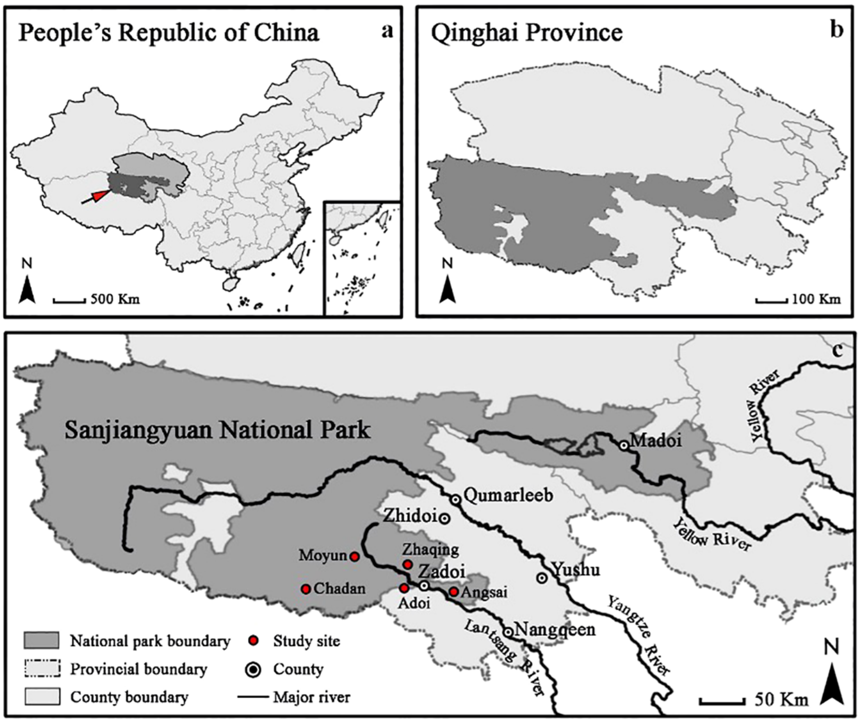

FIGURE 1
Location of Sanjiangyuan National Park in China **(A)**; in Qinghai Province **(B)**; and the study sites **(C)**.

respect, and compassion for all living things. These tenets are shared among those who support nature conservation (Karmapa and Dorje, 2011). The Buddhist faith is an important driver to maintain biodiversity (Shen et al., 2015) since it imparts a sanctity that encourages protection of wild species (James and Cooper, 2007). SNP was once a vast wilderness and a paradise for wildlife, but now the interaction between humans and the environment have led to many conflicts, especially for large carnivores because of their extensive range and dietary needs often overlapping with human activities (Su et al., 2023). The Tibetan brown bear (*Ursus arctos pruinosus*) and gray wolf (*Canis lupus*) are the main species who experience conflict because they kill livestock, destroy houses, and injure people (Dai et al., 2020). Most local people at SNP can tolerate carnivores killing free-range livestock, but bodily injury and house damage are harder to accept (Dai et al., 2019). Conflicts worsen this relationship between locals and wild animals, exhibited by retaliatory actions of residents toward carnivores which threatens species survival (Northrup et al., 2012; Miller et al., 2016; Proctor et al., 2018). As a consequence of these conflicts, the attitudes and behaviors of locals are complex, influenced by publicity for protection, religious and cultural backgrounds, intrinsic value and significance of wildlife, and economic losses caused by these conflicts (Dickman et al., 2011; Kansky and Knight, 2014; Gebresenbet et al., 2018; Tang et al., 2023).

Promotion of flagship or umbrella species is a strategy used by conservationists to achieve sustainable development goals (Brambilla et al., 2013). Flagship species often refer to 'known charismatic species that serve as a symbol or focus point to raise environmental consciousness' (Home et al., 2009). However, the criteria for designating a species as flagship is controversial, on the whole, charismatic species have three attributes: ecological (ethological perspective on the human/environment perception), aesthetic (referring to species behavior or appearance, thus dealing with human emotions), and corporeal (referring to 'affection and emotions engendered by different organisms in their practical interactions with humans') (McGowan et al., 2020; Lundberg and Arponen, 2022). As compared to ecosystem protection, establishing a flagship species is more attractive to the public, which can result in more habitat conservation (Abigail, 2000; Assandri et al., 2017). Flagship species also serve as indicators for conservation outcomes since they increase public awareness and attitudes for endangered species and generate financial support (Bowen-Jones and Entwistle, 2002; Caro et al., 2004). Threatened, charismatic species, usually large vertebrates, have been used as a symbol and rally point for projects, issues, and campaigns (Walpole and Leader-Williams, 2002), thus uniting people to prioritize conservation (Liordos et al., 2017; Thompson and Rog, 2019; Kim et al., 2021). Flagship species, combined with community-based projects, promote attitudinal and behavioral changes of locals, especially if used by the non-governmental organizations (NGOs) as incentives for conservation (Kanagavel et al., 2014; Polgar and Jaafar, 2018).

We used a choice experiment (CE) method to explore the attitudes and perceptions of local Tibetans toward flagship and non-flagship species at SNP in the context of human-wildlife conflict. Our purpose was to assess: 1) community perspectives of endangered species and the emotion and belief basis for participation in conservation; 2) differences in species preference and the heterogeneity of community groups using socioeconomics background; 3) the welfare value of endangered species based on integrated attributes (species importance and degree of conflict); 4) and to propose some viable solutions for community-involved species conservation.

2 Materials and methods

2.1 Study area

Sanjiangyuan National Park (SNP) is located in the hinterlands of the Qinghai-Tibet Plateau. It is a vast area of 190,700 km^2, occupying 26.4% of the total area of Qinghai province (Figure 1). Elevation ranges between 3,335 to 6,564 m, ranging from snow mountains to high-altitude wetlands, forest, rivers, lakes, and grasslands. Known as the "water tower of China," Sanjiangyuan is the source of three great rivers: the Yangtze River, Yellow River, and Lanstang (Mekong) River. SNP is the world's largest, highest, and most concentrated water resource region, including more than 180 rivers, 16,500 lakes, 66,600 km^2 of freshwater marsh, and 1812 km^2 of glaciers (Fan and Fang, 2020). Ecological restoration measures enhance water retention and withstand grassland degradation (Li et al., 2018a).

SNP has a large proportion of threatened and endangered species, including 32.26% mammals and 19.90% birds respectively (Zhang et al., 2023). About 47 mammal species are distributed in SNP, and most of them are endemic to the Qinghai-Tibet Plateau. In addition to Snow leopard (*Pristine plateau*), other carnivores include Gray wolf (*Canis lupus*), Tibetan brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), Tibetan fox (*Vulpes ferrilata*), Chinese mountain cat (*Felis bieti*) and Pallas' cat (*Otocolobus manul*). Main ungulates include Tibetan antelope (*Pantholops hodgsonii*), wild yak (*Bos mutus*), Tibetan wild donkey (*Equus kiang*), White-lipped deer (*Przewalskium albirostris*), Blue sheep (*Przewalskium albirostris*), Tibetan red deer (*Cervus elaphus wallichii*), and Alpine musk deer (*Moschus chrysogaster*).

2.2 Choice experiment design

The choice experiment (CE) is suitable for evaluating awareness and preferences using marginal willingness to pay (MWTP) for improving programs based on the current situation, followed by a series of options or scenarios which contain different attributes and levels on a specific topic (García-Llorente et al., 2012; Lee and Wang, 2017). The theory of CE is based on the consumer theory and random utility theory of economics, among which multinomial Logit model (MNL), random parameter Logit model (RPL) and latent classification model (LCM) are widely used in CE research (Nguyen et al., 2022). Therefore, respondents can select preferred choice sets to make "optimal" decisions rationally, instead of relying on estimations created by statistical models (Sriarkarin and Lee, 2018). Protected area managers find this decision-making approach to be useful for revealing stakeholder opinions and values associated with conservation actions regarding endangered species (Lew and Wallmo, 2017) and to assess policies for community-participative management actions and human-wildlife conflict solutions (Tait et al., 2016).

As applied to this study, we selected five important species at SNP as CE model attributes for evaluating local preferences for endangered species conservation, and divided them to two groups: flagship and non-flagship species. We collected species information at SNP from the literature and through focus group discussions with local managers, NGOs, and biological conservation scholars (Nawaz et al., 2008; Zong et al., 2017; Sriarkarin and Lee, 2018; Lee et al., 2019a). A relatively wide range of physical, ecological and cultural characteristics were used to determine flagship species (McGowan et al., 2020): 1) ecological importance, being representatives for promoting endangered species protection in the ecosystem; 2) attractive or symbolic appearance, having cultural significance for local people (Jepson and Barua, 2015; Senzaki et al., 2017); and 3) generate positive attention for agencies and appeal for collective participative conservation action (Liordos et al., 2017; Lundberg et al., 2020).

Snow leopards, some of the most attractive large felids are distributed in Central Asia mountains. They are representative of snow mountains and plateaus and are important endangered species according to many people and institutions, worldwide (Schutgens et al., 2019; Yang et al., 2021). White-lipped deer are found only in Qinghia-Tibet Plateau and the surrounding areas of alpine forest and grassland in China, known as ‘sacred deer’ by locals. Snow leopards and white-lipped deer have special ecological status in SNP. Tibetan brown bears are an endemic subspecies of the Tibetan Plateau, They are large and fierce omnivores, often considered as the most dangerous animals because they destroy houses and injure people (Worthy and Foggin, 2008; Wu, 2014). It has a unique ecological value, and has an important impact on the relationship between human and wildlife in the SNP area. So, these three species were chosen as flagship species. Blue sheep and gray wolves, which are not flagship species in the SNP area, both in terms of public subjective evaluation and ecological importance, they’re not as charming as snow leopards, white-lipped deer and Tibetan brown bears. All five species represent the Qinghai-Tibet Plateau ecosystem and are familiar to local people. Each are important in the endangered species protection plan and for managing human-wildlife conflict at SNP.

Levels of attributes were determined for each of the five species using information regarding their conservation targets and status. Levels of national key protected wildlife of China were used because local people are familiar with this category but hardly know IUCN protection levels of endangered species in Red List. China’s legal protected wildlife are divided into first-class and second-class species by the department of wildlife administration under State Council. These species have high ecological, scientific, cultural and social value, including endangered, precious and rare species, and species with high intensity of exploitation and utilization (Jiang, 2016). These two categories of protected species in China include 686 terrestrial wildlife, and only part of them belong to IUCN’ threatened species (Huang et al., 2021). SL and WLD are first-class, national key protected species with 3 levels of conservation attributes, and Tibetan Brown Bear (TBB), Blue Sheep (BS) and Gray Wolf (GW) are second-class national key protected species with 2 levels (Table 1). The conservation target of these species at SNP was to recover endangered species populations, and for first-class species Snow Leopard (SL) and White Lipped Deer (WLD) the periodic target was to improve their conservation status.

We designed scenarios for alternative programs by assuming that relevant institutions would set up a conservation trust fund for endangered species. To determine the value of conservation fund options, we delivered 50 pre-survey questionnaires to local respondents, and entered the funding amount they deemed appropriate for sum of species conservation. The numerical

TABLE 1 Attributes and levels for endangered species conservation in Sanjangyuan National Park.

Attributes	Levels	Variables	Types
White Lipped Deer (WLD)	a. Status quo: Class I National key protected species (IUCN, VU)	WLD±	Flagship species
	b. Improve conservation status by reducing threats	WLD1	
	c. Recover the population through conservation efforts	WLD2	
Snow Leopard (SL)	a. Status quo: Class I National key protected species (IUCN, VU)	SL±	Flagship species
	b. Improve conservation status by reducing threats to SL	SL1	
	c. Recover the population through conservation efforts	SL2	
Tibetan Brown Bear (TBB)	a. Status quo: Class II National key protected species (IUCN, LC)	TBB±	Flagship species
	b. Recover the TBB population to non-threatened species	TBB	
Blue Sheep (BS)	a. Status quo: Class II National key protected species (IUCN, LC)	BS±	Non-flagship species
	b. Recover the population through conservation efforts	BS	
Gray Wolf (GW)	a. Status quo: Class II National key protected species (IUCN, LC)	GW±	Non-flagship species
	b. Recover the population through conservation efforts	GW	
Conservation fund	a. Status quo: no conservation fund	FUND*	
	b. 250 RMB/household/year		
	c. 500 RMB/household/year		
	d. 750 RMB/household/year		
	e. 1000 RMB/household/year		

*FUND is a financial attribute, means fund for biodiversity conservation, and RMB means Chinese Renminbi (Yuan).

values were ranked from lowest to highest and percentiles of 24%, 42%, 58% and 72% were selected as the grades of four groups of conservation trust funds (250RMB, 500RMB, 750RMB, and 1,000RMB) (Table 1). Through SPSS orthogonal experiment, 25 level combinations were generated. After eliminating unreasonable options, 19 combinations and 1 status quo remained, resulting in 66 paired choice sets. Each version of the questionnaire consisted of 3 choice sets, and each choice set included 2 alternative programs for a total of 26 versions of the questionnaire (Table 2). Questionnaires (Supplementary Data) consisted of three parts: 1) cognition and attitude toward the endangered species and its conservation; 2) conservation preference for the endangered species at SNP; 3) social-economic data and information on human-wildlife conflict.

2.3 Survey implementation

We conducted a survey in Lanstang river source of SNP during April to July of 2018. Investigation sites included 5 towns of Zadoi county, in Yushu Tibetan Autonomous Prefecture of Qinghai Province, respectively are Chadan, Moyun, Zhaqing, Adoi and Angsai (Figure 1). We sampled households randomly at 19 villages, asking only one individual per household to complete the questionnaire. Because more than 90% of the residents were Tibetan, and the second part of questionnaire was difficult to understand, we hired Tibetan translators. During face-to-face interviews, the investigators explained the scenarios of endangered species conservation, the meaning of choice set, and the alternative programs of different level combinations, so that respondents could match suitable options with their own opinions. A total of 26 versions of the questionnaire were used. We visited 416 residents and collected 409 valid questionnaires (98.3% response), consisting of 110 in Zhaqing, 89 in Moyun, 85 in Chadan, 73 in Angsai and 52 in Adoi township.

2.4 Statistical analysis

Random parameter logit (RPL) and latent class model (LCM) were used to explore the local preferences and heterogeneity for conservation options with endangered species. The models were built using NLOGIT 5. The RPL model evaluated each attribute in relation to heterogeneous preferences and welfare (Sriarkarin and Lee, 2018; Lin et al., 2020). Coefficients from RPL were used to calculate MWTP from potential scenarios of attributes and levels (Lee et al., 2019b; Lin et al., 2020; Wang et al., 2020). LCM can subdivide respondents into different classes based on preferences and socio-economic perspectives to determine explicit management policies (Juutinen et al., 2011; Lee et al., 2019b; Lin et al., 2020).

In the RPL model. Local preferences for endangered species conservation can be expressed as Equation (1):

$$V_{ni} = \beta_1 WLD_i + \beta_2 SL_i + \beta_3 TBB_i + \beta_4 BS_i + \beta_5 Wolf_i + \beta_6 Conservation\ \ fund_i \tag{1}$$

Where $\boldsymbol{V_{ni}}$ the utility function linked with alternative i, β_i is the estimated coefficient of alternative i, and WLD_i, SL_i, TBB_i, BS_i, $Wolf_i$ and $Conservation\ \ fund_i$ represent attribute vector coefficients. Results of the RPL model were used to calculate the marginal welfare effects. the values of community marginal conservation fund for five endangered species are calculated as the ratio of two parameters associated with the attribute ($\beta_{attribute}$) and the estimated coefficient of the monetary attribute (β_c), as shown in Equation (2):

$$Marginal\ \ conservation\ \ fund_{per\ \ attribute} = \frac{\beta_{attribute}}{\beta_c} \tag{2}$$

Where $\boldsymbol{\beta_{attribute}}$ is the coefficient of local preference for endangered species conservation, and $\boldsymbol{\beta_c}$ is the coefficient of conservation fund.

TABLE 2 Example of a choice set for locals' preferences toward endangered species conservation (Red, yellow and green represent the different levels for conservation and recovery of these species).

Choice set 1	Program 1「Additional conservation action」	Program 2「Additional conservation action」	Status quo「No additional conservation action」
White-lipped Deer	Status quo—**First-class** national key protected species	**Recover the population** through conservation efforts	Status quo—**First-class** National key protected species
Snow Leopard	**Improve conservation status** by reducing threats	Status quo—**First-class** national key protected species	Status quo—**First-class** national key protected species
Tibetan Brown Bear	Status quo—**Second-class** national key protected species	Status quo—**Second-class** national key protected species	Status quo—**Second-class** national key protected species
Blue Sheep	Status quo—**Second-class** national key protected species	Status quo—**Second-class** national key protected species	Status quo—**Second-class** national key protected species
Gray Wolf	**Recover the population** through conservation efforts	Status quo—**Second-class** national key protected species	Status quo—**Second-class** national key protected species
FUND	$750 RMB/person/year	$250 RMB/person/year	—
CHOICE	☐	☐	☐

3 Results

3.1 Attitudes and cognition to endangered species conservation

The sample consisted mostly of males (71.8%) since they were more willing to be interviewed than females (28.2%). However, gender was non-significant (*Pearson Chi-Square test, $\chi2 = 1.576$, df=1, p=0.209*, using a 95% confidence interval). Overwhelmingly, respondents were from Tibet (96.1%) and most of them (54.4%) attended a Tibetan language school. Education levels were comparatively low: 50.9% primary school education or lower. Over two-thirds (68.5%) of respondents have lived in community for more than 10 years (for more information on socioeconomics of respondents, see Table 3). Over half (59.9%) of the households had annual incomes of more than 50,000 RMB, mostly from cordyceps (*Cordyceps militaris*) (87.3%). Others had monthly wages (30.3%), grassland awards and subsidies (25.2%), turf income (12.5%), and subsidies for poor households (9.5%).

Regarding the cognition of conservation status and willing to protect endangered species, Snow leopard scored the highest (92.4% and 99.3% respectively), white lipped deer and blue sheep had lower cognition (77.3% and 75.8%) and higher willingness (99.3% and 99.5%). Fewer respondents knew that Tibetan brown bears and gray wolves were second-class national key protected animals (68.7% and 60.6%, respectively) and willing to protect them (86.6% and 85.8%, respectively). Over three-fourths (81.9%) of the respondents were concerned about endangered wildlife conservation, and they had more positive attitudes toward the protective effect of national park, and participating to protect these species (see the first three group of bars, Figure 2). Factors prompting wildlife protection mainly consist of religious beliefs (93.4%), national regulations and policies (89%), contact with nature (77.3%), family tradition and inheritance (76.3%), and guidance by NGOs (67.7%) (see the fourth to eighth group of bars, Figure 2).

TABLE 3 Basic social-economics information of locals' respondents.

Characteristics	All respon-dent (n=409)	Concern about the topic of endangered species conservation	
		Yes (n=335)	No (n=74)
Gender			
Male	294 (71.8%)	245 (73.1%)	49 (66.2%)
Female	115 (28.2%)	90 (26.9%)	25 (33.8%)
Age			
20-29 years old	91 (22.3%)	80 (23.9%))	11 (14.9%)
30-39 years old	117 (28.6%)	98 (29.2%)	19 (25.7%)
40 years old and elder	201 (49.1%)	157 (46.9%)	44 (59.4%)
Education level			
Primary school and under	208 (50.9%)	162 (48.4%)	46 (62.2%)
Junior and senior high school	56 (13.7%)	52 (15.5%)	4 (5.4%)
College and above	145 (35.4%)	121 (36.1%)	24 (32.4%)
Family size			
1-3 people	95 (23.3%)	80 (23.9%)	15 (20.3%)
4-6 people	212 (51.8%)	175 (52.2%)	37 (50.0%)
More than 6 people	102 (24.9%)	80 (23.9%)	22 (29.7%)
Household annual income			
50, 000RMB and under	395 (96.6%)	325 (97.0%)	70 (94.6%)
50, 000-100, 000RMB	13 (3.2%)	10 (3.0%)	3 (4.1%)
100, 000RMB and above	1 (0.2%)	0 (0.0%)	1 (1.3%)
Residence length in the community			
1-10 years	129 (31.5%)	102 (30.4%)	27 (36.5%)
11-20 years	187 (45.7%)	160 (47.8%)	27 (36.5%)
More than 20 years	93 (22.8%)	73 (21.8%)	20 (27.0%)
Raise domestic livestock or not			
Yes	130 (31.8%)	100 (29.9%)	30 (40.5%)
No	279 (68.2%)	235 (70.1%)	44 (59.5%)
Join environmental group or not			
Yes	110 (26.9%)	89 (26.6%)	21 (28.4%)
No	299 (73.1%)	246 (73.4%)	53 (71.6%))
Know the conservation and monitoring institutions of endangered species [a]			
Yes	328 (80.2%)	291 (86.9%*)	37 (50.0%*)
No	81 (19.8%)	44 (13.1%*)	37 (50.0%*)
Willing to donate money to endangered species conservation [b]			
Agree and strongly agree	316 (77.3%)	272 (81.2%*)	44 (59.3%*)
Neutral	80 (19.6%)	54 (16.1%*)	26 (35.1%*)
Disagree and strongly disagree	13 (3.1%)	9 (2.7%*)	4 (5.4%*)

a: $\chi^2 = 31.723$; P=0.000; b: $\chi^2 = 11.031$; P=0.004

The relationship between humans and wild animals was discussed during the face-to-face interviews. Two-thirds of respondents (66.5%) think that wildlife damage results in trouble. Main conflicts included: 53.3% destruction of houses and other property by Tibetan brown bears; 27.3% livestock injured or killed by snow leopards or wolves; 18.1% human injury mostly by bears; and 8.6% ungulates competing with livestock for grass.

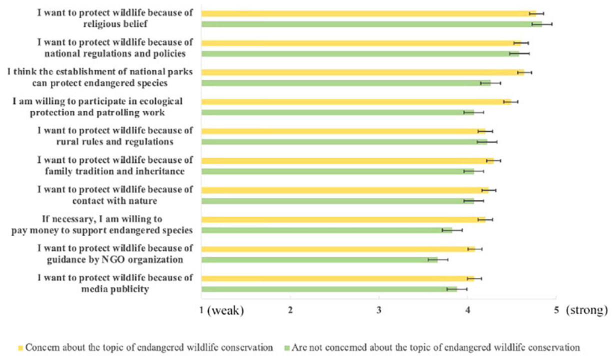

FIGURE 2
Local' attitudes to endangered species conservation, participation, and wildlife protection motivators.

3.2 Local preferences for endangered species conservation

The log-likelihood ratio (LLR) indicated that our RPL models had a high fitness for endangered species protection preference estimation since nearly all the attributes and levels were significant including conservation fund after the interaction with FUND (Table 4). Results from the RPL model showed that respondents would like to select additional conservation actions rather than status quo. Local people were more inclined to support population recovery for SL, WLD and BS, than improve conservation status of SL and recover the GW population. Yet TBB population recovery was not supported. Willingness to contribute to the conservation fund goes down as the amount goes up. Moreover, the coefficient of interaction between FUND with D4, D6 and D3 was significant, meaning that residents who are Tibetan, with annual household incomes not higher than 70000RMB, think wild animals can injure livestock, and were more reluctant to support a conservation fund for endangered species.

The welfare effect of endangered species conservation was estimated based on marginal conservation fund. For flagship species conservation, the highest value of Mean WTP was recovering WLD population (361.4 RMB/household/year, 95% CI 340.8~381.9), followed by the SL population (308.8 RMB/household/year, 95% CI 289.1~312.5). However, the Mean WTP of recovering TBB population had a negative value (-91.8 RMB/household/year, 95% CI -125.9~57.7). For results of non-flagship species, recovering the BS population got more conservation fund support (234.8 RMB/household/year, 95% CI 138.3~331.3) than

TABLE 4 Estimation results of Random Parameter Logit Model.

Attributes and levels	Coefficient (*t* Value)	Coef. Std. (t value)	Attributes and levels	Interaction with FUND	
				Coefficient (t value)	Coef. Std. (t value)
WLD1	-0.159 (-0.940)	1.398 (2.190)**	WLD1	-0.198 (-1.140)	0.909 (2.090)**
WLD2	2.355 (2.880)***	0.911 (1.420)	WLD2	2.812 (3.590)***	0.783 (0.960)
SL1	0.415 (2.200)**	0.577 (1.300)	SL1	0.565 (2.810)***	0.327 (0.580)
SL2	1.455 (2.900)***	0.301 (0.340)	SL2	1.775 (3.710)***	0.270 (0.370)
TBB	-0.592 (-2.510)**	0.375 (0.590)	TBB	-0.714 (-3.060)***	0.973 (1.970)**
BS	1.553 (2.810)***	1.501 (2.320)**	BS	1.826 (3.520)***	1.680 (2.830)***
GW	0.239 (2.070)**	0.807 (1.550)	GW	0.322 (2.560)**	0.839 (1.730)*
FUND	-0.001 (-0.890)	0.000 (0.020)	FUND	-0.008 (-2.530)**	0.000 (0.110)
			D1*FUND	0.001 (0.760)	0.000 (0.020)
			D2*FUND	-0.001 (-1.120)	0.000 (0.050)
			D3*FUND	0.003 (1.700)*	0.014 (3.250)***
			D4*FUND	0.007 (2.590)***	0.000 (0.040)
			D5*FUND	0.001 (0.790)	0.000 (0.040)
			D6*FUND	-0.002 (-2.219)**	0.000 (0.130)
Log-likelihood ratio	825.427		Log-likelihood ratio	887.610	
Chi Square	$\chi^2_{0.01}$ (16) = 23.540***		Chi Square	$\chi^2_{0.01}$ (28) =37.920***	

***, **, * ==> significance at 1%, 5%, and 10% level, respectively. D1: Know the conservation and monitoring institutions of endangered species; D2: Willing to donate money to endangered species conservation; D3: Think wild animals injure livestock; D4: Tibetan; D5: Junior high school and under; D6: Annual household income higher than 70000 RMB.

that of the GW population (41.5 RMB/household/year, 95% CI 12.5~70.5). In general, locals were willing to pay more for conserving flagship species than non-flagship species, but not including conflict species.

3.3 Preference heterogeneity based on community perspectives

Results from the LCM analysis showed heterogeneity after incorporating social-economic variables into the model and segmenting respondents into three types by their preferences (Table 5). Over half of the locals (56.0%) are multi-species conservation seekers who prefer a variety of animals except for Tibet brown bears (without significant t value). The second type (30.7%) of individuals have strong preference and conflict simultaneously. They prefer fund to WLD, BS and SL population recovery, but dislike TBB and GW, and disapprove the conservation status of two first class national key species. The third type is also the smallest group (13.3%). They are less concerned about endangered species conservation, only willingness to recover WLD population and dislike TBB, and exhibit a lack of preference for other species.

Heterogeneity of community perspectives can be useful for distinguishing separate groups based on social-economic characteristics (Table 6). The group of multi-species conservation includes more people with higher household income for contributing to the protection of endangered species due to religious beliefs. In contrast, people in the other two groups have lower household income. The group that has the least amount of conservation concern consists of those who are less focused on endangered species conservation and who know little about the agencies who protect and monitor them. These residents suffered more human-wildlife conflict issues (i.e., they think wild animals

TABLE 5 Estimation results of Latent Class Model.

Attributes and Levels	Class I (56.0%) Multi-species conservation		Class II (30.7%) Strong preference and conflict		Class III (13.3%) Less concern to conservation	
	Coefficient	*t* value	Coefficient	*t* value	Coefficient	*t* value
WLD1	0.771***	3.110	-3.240***	-3.660	-0.619***	-2.820
WLD2	1.960***	5.230	4.560***	3.900	0.729***	3.040
SL1	1.89***	4.750	-3.860***	-2.960	0.005	0.040
SL2	1.98***	6.870	1.480***	2.970	0.107	0.430
TBB	0.475	1.500	-1.840***	-3.840	-0.373**	-2.050
BS	1.190***	6.050	3.190***	4.220	0.077	0.570
GW	0.753***	4.600	-1.170***	-2.670	0.111	0.790
FUND	-0.009***	-4.280	0.017***	3.570	0.002**	2.150
Parameters			Class I		Class II	
			Coefficient	*t* value	Coefficient	*t* value
Constant			-10.540**	-2.010	-10.710**	-2.030
Gender			-6.220	-0.930	-6.680	-1.000
Age			10.890	1.410	10.670	1.380
Tibetan			16.330*	1.920	16.270*	1.910
Annual household income above 70,000 RMB			14.590*	1.760	13.930*	1.680
Concern about the topic of endangered animal conservation			15.110*	1.820	15.640*	1.880
Think wild animals injure livestock			-25.150*	-1.600	-25.950*	-1.650
Think wild animals compete with livestock for grass			27.560*	1.720	28.080*	1.750
Number of choice sets			1227.000			
Log-likelihood Ratio			980.110			
Chi Squared			$x^2_{0.01}(40)= 51.800$***			

***, **, * ==> significance at 1%, 5%, and 10% level, respectively.

TABLE 6 The cross comparison for clusters and attributes of locals' attitude towards endangered species conservation.

Clusters	Multi-species conservation	Strong preference and conflicts	Less concern to conservation
Variables	Frequency (Percentage)		
Annual household income (RMB)			
Higher than 70,000	151 (60.6)	27 (28.1)	16 (25.0)
Lower than 70,000	98 (39.4)	69 (71.9)	48 (75.0)
Chi-square=44.69*			
Tibetan or not			
Yes	244 (98.0)	94 (97.9)	55 (85.9)
No	5 (2.0)	2 (2.1)	9 (14.1)
Chi-square=9.15*			
Concern about the topic of endangered species conservation			
Yes	211 (84.7)	89 (92.7)	36 (56.2)
No	38 (15.3)	7 (7.3)	28 (43.8)
Chi-square=40.9*			
Know the conservation and monitoring institutions of endangered species			
Yes	213 (85.5)	79 (82.3)	36 (56.3)
No	36 (14.5)	17 (17.7)	28 (43.8)
Chi-square=27.85*			
Raise domestic livestock			
Yes	72 (28.9)	22 (22.9)	36 (56.3)
No	177 (71.1)	74 (77.1)	28 (43.8)
Chi-square=22.09*			
Think wild animals injure livestock			
Yes	50 (20.1)	4 (4.2)	58 (90.6)
No	199 (79.9)	92 (95.8)	6 (9.4)
Chi-square=7.65*			
Think wild animals hurt people			
Yes	28 (11.2)	18 (18.8)	28 (43.8)
No	221 (88.8)	78 (81.3)	36 (56.3)
Chi-square=36.33*			
Think wild animals destroy house and other property			
Yes	116 (46.6)	52 (54.2)	50 (78.1)
No	133 (53.4)	44 (45.8)	14 (21.9)
Chi-square=20.38*			
Willing to donate money to endangered species conservation			
Disagree and strongly disagree	3 (1.2)	3 (3.1)	7 (10.9)
Neutral	39 (15.6)	23 (24.0)	18 (28.1)
Agree and strongly agree	207 (83.2)	70 (72.9)	39 (61.0)
Chi-square=24.90**			

(Continued)

TABLE 6 Continued

Clusters Variables	Multi-species conservation	Strong preference and conflicts	Less concern to conservation
	Frequency (Percentage)		
Protect wildlife for the reasons of religious belief			
Disagree and strongly disagree	5 (2.0)	2 (2.1)	1 (1.6)
Neutral	41 (16.5)	35 (36.5)	20 (31.3)
Agree and strongly agree	203 (81.5)	59 (61.4)	42 (65.6)
Chi-square=27.90**			
Protect wildlife because of the guidance of NGOs			
Disagree and strongly disagree			
Neutral	3 (1.2)	2 (2.1)	4 (6.3)
Agree and strongly agree	72 (28.9)	30 (31.3)	21 (32.8)
Chi-square=16.42**	174 (69.9)	64 (66.7)	39 (60.9)

*$\chi^2_{0.05}$ (2) =5.99, P<0.05. **$\chi^2_{0.05}$ (4) =9.49, P<0.05.

injure livestock, destroy houses and other property), because most of them raise domestic livestock. The group consisting of strong preference and conflict shared similar characteristics with the first group, i.e., those who are concerned about species conservation, but they also have more conflicts with Tibetan brown bears (because they destroy houses and hurt people; Table 6).

4 Discussion

4.1 Flagship species conservation preference and the impacts of human-wildlife conflicts

Successful biodiversity conservation requires stable and reliable support from local people, rooted in positive attitudes and awareness for endangered species, which influence their behavior and participation for protection (Addison et al., 2016; Colléony et al., 2017). Conservation awareness of community residents is important since it will help them understand the existing problem and what can be done to protect the endangered species (Baharum et al., 2017; Jalil and Mat Sharif, 2018). If positive, public opinion on flagship species can increase fundraising and improve conservation targets and ecosystem services (Senzaki et al., 2017; Gonga et al., 2020). Conservation awareness can be raised through effective policy implementation and appropriate incentives for information dispersal aimed at enhancing attitudes toward flagship species (Barua et al., 2010; Thompson and Rog, 2019). Yet the effectiveness of this approach for promoting regional biodiversity is controversial in many regions worldwide who invest large sums of money for conservation efforts (Sergio et al., 2008; Timmer et al., 2019).

Our results showed that snow leopards, as a symbolic endangered species at SNP, generated the most concern and support for protection. They also received the greatest preference for population recovery and conservation status improvement. Welfare values of snow leopards and white-lipped deer are higher than other non-flagship species. Most respondents were concerned about conserving endangered species and the relevant agencies for managing them. In other words, positive attitudes and perceptions benefit species conservation strategies at SNP and local governments (Li et al., 2013; Qian et al., 2020; Dai et al., 2022). For non-flagship species (such as BS and GW), conservation preference and MWTP value were also high, indicating that less popular species can reflect local support for conservation (Veríssimo et al., 2017). This is noteworthy when compared against unique "charismatic" species. Tibetans have a tradition of protecting all life, meanwhile special conservation and management measures are implemented to snow leopards and white-lipped deer because of their important ecological status in SNP. There are some examples for different conservation preference of public to different kinds of species (Wallmo and Lew, 2012; Garnett et al., 2018; Lundberg et al., 2019). Improving media propaganda, knowledge and attitudes of locals would benefit the conservation of non-flagship species (Curtin and Papworth, 2018; Shreedhar and Mourato, 2019).

But not all flagship species at SNP have local support. Aversion to the Tibetan brown bear illustrates the seriousness of human-wildlife conflict for endangered species conservation. Over half of the respondents (53.3%) reported house damages with little compensation. Human-bear conflict has emerged as a severe problem, complicated by Tibetan Buddhism. Herdsmen at SNP leave dead livestock in the fields which easily attract brown bears who are naturally drawn the to smell of carrion. This food source brings them closer to residential areas, thus increasing the risk of house damage, especially during the winter. Bears also threaten the livelihood and safety of local herders, decreasing community tolerance for Tibetan brown bear conservation (Dai et al., 2020). Therefore, attitude change regarding bears is a hindrance for conservation outcomes at SNP, something that should be evaluated from ecological and social-economic aspects (Molina et al., 2019; Lundberg et al., 2020). Conflict mitigation measures should include house protection and reinforcement, guiding residents to dispose of dead livestock properly, developing compensation programs, and creation of insurance policies. Park rangers should focus on bear education and their ecological importance, but also explain causes of conflict and defense strategies for local communities.

4.2 Conservation preference heterogeneity of different community groups

Demographics and socio-economic factors were entered into LCM as categorical variables (Alegre et al., 2011; Juutinen et al., 2011; Sriarkarin and Lee, 2018). They included: gender, age, household annual income, Tibetan or not, endangered species conservation attitudes (Li et al., 2013), human-wildlife conflicts (Zong et al., 2017; Cai et al., 2020). Our results showed heterogeneity of endangered species conservation preferences in local communities, which were significant among groups with different social-economic background and conservation attitudes.

The highest proportion of respondents is ‘multi-species conservation seekers’ who prefer nearly all species with multiple levels and ecological status. They have higher annual incomes, lower impacts from wildlife, highest awareness, and contribution to endangered species, and the most religion reasons for participating in conservation. On the contrary, the ‘less concern to conservation’ group only focused on conservation of a few species and have no strong attitudes. They have the highest negative impacts from wildlife, lowest concern for endangered species, lower awareness of conservation institutions, less willing to contribute money for conservation, and less support for NGOs. The ‘strong preference and conflict’ group has strong likes and dislikes to endangered species. They are most concerned about the topic of endangered species conservation but have incurred the most house damage by bears. The common characteristics of the latter two groups is comparatively low household incomes, fewer religious beliefs, and much more conflicts with wild animals.

The ‘strong preference and conflict’ group account for certain proportion of locals. They dislike Tibetan brown bear and wolves very much but are willing to protect lower-conflict species like snow leopard, white-lipped deer, and blue sheep. Except for bears, killing livestock by wolves is the main cause of conflict, leading to poaching and retaliatory killings (Fowler et al., 2019; Estifanos et al., 2020; Janeiro-Otero et al., 2020; Kirilyuk and Ke, 2020). Due to the livestock loss caused by wolves, local herdsmen showed negative behavior by killing wolves with poison or traps, which also unintentionally kills snow leopards (Qian et al., 2020). Economic loss caused by animals is the main driver of human-wildlife conflict (Li et al., 2018b; Horgan and Kudavidanage, 2020; Siljander et al., 2020). If annual income is low, it is difficult for people to accept conflict without retaliation (Kleiven et al., 2004). Implementation of preventive measures, damage compensation and insurance policies are important to the “strong preference and conflict” group for changing their attitude toward conservation and coexistence with these species (van Eeden et al., 2021).

4.3 Implication to community-participative conservation action of SNP

Community participation is important for biodiversity conservation at national parks in China. Endangered species protection can be a source of community well-being, productivity, tourism, or connections with nature (Naeem et al., 2016). It provides residents with material welfare for their livelihoods and contributes to resiliency, security, social relations, health, and freedom of choice (Christie et al., 2006; Milkisso, 2020). Economic incentives, livelihood assistance, non-economic and intrinsic motivation are some of the reasons for community-based participation at SNP (Martín-Loípez et al., 2007). Knowledge, attitudes, and behavior of Tibetans are influenced by their spiritual values and religious beliefs of sacred mountains and lakes, combined with their ethnic tradition (Dudley et al., 2009). The idea of a wilderness cult may make a significant contribution to protection of endangered species and biodiversity (Mgumia and Oba, 2003; Bhagwat et al., 2005a, b; Bossart et al., 2006), so factors such as Tibetan culture and religious beliefs can be incorporated into adaptive conservation policies.

Our results suggest implications for a conceptual framework of endangered species conservation under community perspectives (Figure 3). Different conservation preferences for flagship and non-flagship species and the heterogeneity of different groups can be used to improve conservation efforts at SNP. The main community-involvement conservation actions are mitigating human-wildlife conflicts and increasing internal and external motivators to find a suitable balance between them (Tang et al., 2023). The goal of maintaining ecosystem integrity at national parks can be achieved by using flagship species or flagship fleets for promoting community-participative plans while addressing local conservation preferences and heterogeneity (Hemson et al., 2009; Veríssimo et al., 2014a; Lundberg et al., 2020). Other protected area studies also support this viewpoint (Zong et al., 2017; Sriarkarin and Lee, 2018; Lee et al., 2019).

We found that heterogeneity of conservation preference is influenced by household income, traditional ethnicity culture, and conservation awareness (Wiepking and Bekkers, 2012). Dividing individuals into groups with similar preferences helps governments, managers, and NGOs to develop strategies for communities (Veríssimo et al., 2014). For example, the ‘multi-species

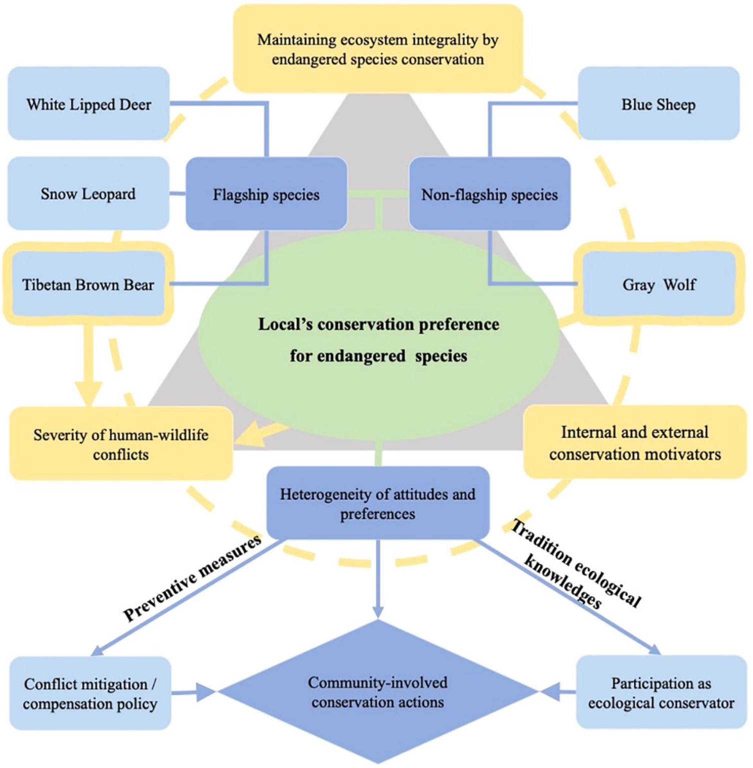

FIGURE 3
Conceptual framework of community participation consevation in Sanjiangyuan National Park.

conservation seekers' with strong preferences for wildlife protection were more willing to participate in endangered species conservation. Ecological conservator plans at SNP requires public support to monitor wild areas by patrols, so community-based conservation underscored the importance of involving this segment of people. Our study showed that community-involved species conservation at SNP should encourage more community participation mechanisms, conservation education and training for residents, promoting conservation emotive motivators, attaching importance to religious tradition and ethnoecological knowledge (Trudgill, 2001; Li et al., 2018c; Adom and Boamah, 2020; Qian et al., 2020).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

WX: Writing – original draft. LX: Writing – review & editing. YC: Writing – review & editing. JZ: Writing – review & editing. YW: Writing – review & editing. KC: Writing – review & editing. C-HL: Writing – review & editing. HD: Writing – review & editing. SM: Writing – review & editing. CZ: Writing – review & editing.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1265694/full#supplementary-material

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Effectiveness assessment of protected areas based on the states, trends, and relative changes in forest ecosystem: a case study in the Three Parallel Rivers Region, China

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Establishing protected areas (PAs) is a major measure of biodiversity conservation, and various methods have been explored to assess PAs' effectiveness. However, those methods mainly compared the relative changes in land cover between treated samples inside the PAs and their matched samples outside the PAs, which would produce misjudgments, especially in some climax communities with a relatively steady state. Thus, in this study, we constructed an integrated framework through a series of assessments according to the state, trend, and relative change of each PA to explore the conservation effectiveness of PAs in the Three Parallel Rivers Region in China from 2000 to 2020. Here, "state" refers to the difference among samples from within and outside the PA, assessed through yearly sample mean comparison. "Trend" means linear regression of mean forest area of each PA throughout the assessment period. "Relative change" means the difference in the mean value of the slope of forest changes between the treated samples inside each PA and their matched control samples outside of PAs. The entire forest area within all PAs in the Three Parallel Rivers Region showed a significant increasing trend from 2000 to 2020 (R^2 = 0.919, P<0.05). Among all the PAs, twelve (86%) had a positive effect on protecting the forest ecosystem, and two had a nonsignificant effect. Among the factors affecting the state and relative change in PAs' forests, the annual total precipitation was the most important, followed by distance to the nearest road. Moreover, the management-level variable was an essential factor in the state of PAs' forest ecosystems, which indicated that national PAs (nature reserves and natural parks) were in a better state than local (provincial- and county-level) nature reserves. Overall, the conservation effectiveness of forests in PAs was assessed at a regional scale in the Three Parallel Rivers Region, implying that our framework would be additional useful in regions with high biodiversity and steady ecosystems. This framework better avoids underestimating conservation effectiveness assessment tasks than traditional methods do. Thus, we posit that this framework is suitable for future global or country-level assessments.

KEYWORDS

conservation effectiveness, integrated framework, natural park, nature reserve, northwest Yunnan

1 Introduction

Establishing protected areas (PAs) is the main method of defending against biodiversity loss because it conserves vital ecosystems, wildlife, and habitats (Gaston et al., 2008; Stolton and Dudley, 2010). By May 2021, at least 22.5 million km^2 (16.64%) of land and inland water ecosystems were within PAs and Other Effective area-based Conservation Measures (OECMs) (UNEP-WCMC, and IUCN, 2021). Except for fulfilling the quantitative coverage target, it is also important to know whether existing PAs are effectively protecting biodiversity features. For instance, 71.4% of PAs worldwide helped prevent forest loss, without PAs, forest loss within the boundaries of 287 PAs would have increased by 77,857 km^2 between 2000 and 2015 (Yang et al., 2021). With the escalation of environmental crises, evaluating PAs' conservation effectiveness is necessary to guarantee benefits to humankind and ensure that PAs can maintain positive mechanisms to achieve their diverse objectives and realize their full potential (Watson et al., 2014; Di Minin and Toivonen, 2015). The Kunming-Montreal Global Biodiversity Framework, adopted by the 15th Conference of the Parties to the Convention on Biological Diversity, further emphasizes the effectiveness of PAs (UN Environment programme, 2022). Notably, methods have been adopted to assess the effectiveness of PAs, such as "before-after" comparison (Gaveau et al., 2007), "inside-outside" comparison (Wang et al., 2015), these comparisons are often influenced by environmental factors and are not sufficiently scientific. Thus, "matching" methods are gradually being applied to scientifically assess the conservation effectiveness of PAs by eliminating the effects of environmental factors (Ren et al., 2015; Geldmann et al., 2019).

Because of the absence of annual continuous land cover data, previous studies have mostly adopted the method of subtracting two years when making "before-after" comparison to explore the effectiveness of PAs (Bowker et al., 2017; Chen et al., 2017; Geldmann et al., 2019; Mammides, 2020). Studies have mainly assessed PAs' conservation effectiveness by comparing changes in land cover (e.g., forest ecosystems) between treated samples inside PAs and their matched samples outside PAs (Gaveau et al., 2009). In this way, the relative increase of treated samples inside PAs compared to their matched samples outside PAs in land cover (natural vegetation) were able to represent a positive conservation effectiveness. However, few studies have focused on the initial status of conservation effectiveness evaluation. Without initial status, PAs with high human-pressure baselines may appear more effective than those with low baselines under equally stringent pressure conditions (Feng et al., 2022). And when forest area is used to assess conservation effectiveness of PAs, the results may be biased because natural vegetation cannot increase continuously, especially when the forest becomes a climatic community with a dynamic steady state (Meng et al., 2023). In such cases, PAs' conservation effectiveness might be judged as negative, based merely on the relatively stable forest coverage inside PAs being compared with that of the forest ecosystem outside PAs.

The outcomes of conservation effectiveness assessments rely on the available data on PAs (Pereira et al., 2013), and data limitations lead to incomplete results and restrict the potential applicability of previous methods. Nowadays, with the development of remote sensing and monitoring techniques, additional precise and continuous data have been generated, such as forest changes from annual remote sensing datasets (Hansen et al., 2013; Yang and Huang, 2021), making it possible to identify PAs' conservation effectiveness by integrating the state and change in land cover (e.g., forest ecosystems) in a series of periods. According to previous studies, "states" represents the baseline throughout the entire assessment period, refers to the difference of assessment indicators among samples from within and outside the PA (Feng et al., 2022). "Trends" here specifically means whether significant changes occur within the PA throughout the assessment period. And the depiction of conservation effectiveness concerning temporal changes corresponds to "relative changes", which refers to the differences in slopes derived from sample changes within PA relative to those outside over the assessment period (Meng et al., 2023). Related studies have also emphasized the importance of an integrated framework which considers both the basic condition and dynamic comparison (Meng et al., 2023), which could increase the accuracy of conservation effectiveness assessments of PAs.

In this study, we selected the Three Parallel Rivers Region (TPRR) as our study area. The TPRR is one of the global biodiversity and cultural hotspots and a biodiversity epicenter in China and has the richest biodiversity among temperate areas worldwide (United Nations Educational Scientific and Cultural Organization (UNESCO), 2003). Fifteen PAs have been established in the TPRR, namely different levels of nature reserves and natural parks. As forests are the major ecosystem in the TPRR, which is also the basis for realizing the value of PAs and other ecosystem services, assessing conservation effectiveness is necessary to achieve long-term protection goals (Lopoukhine et al., 2012; Wang et al., 2021). Using the Annual China Land Cover Dataset (CLCD) (2000–2020) produced by the Google Earth Engine (Yang and Huang, 2021), we calculated the forest area for each year in the TPRR and every PA established from 2000 to 2020. We then constructed a framework that combined the state, trend, and relative change in forest area to assess the conservation effectiveness of each PA since 2000. Here, “state” refers to the difference among samples from within and outside the PA, assessed through yearly sample mean comparison. “Trend” means linear regression of mean forest area of each PA throughout the assessment period. And “relative change” means the difference in the mean value of the slope of forest changes between the treated samples inside each PA and their matched control samples outside of PAs. Finally, we attempted to identify the critical factors and their influence on the state and changes in forest areas in each PA. Our aim for creating this framework was that it would improve the accuracy of PA conservation effectiveness assessments and thus be adopted in future global or country-level assessments.

2 Materials and methods

2.1 Study area

The TPRR is in the northwest of Yunnan, China (25°30′–29°00′ N, 98°00′–101°31′ E), with a total area of 45,000 km^2. The three rivers are the Yangtze (Jinsha), Mekong (Lancang River), and Nu-Salween, which run parallel from north to south. The region is in the southern part of the Hengduan Mountains, and its topography is characterized by extremely high mountain ranges and deep valleys (Lin et al., 2016). The TPRR contains subtropical, temperate, cold temperate, cold mountain, dry-hot valley, wetland, and aquatic vegetation types (Zhang et al., 2013), which are vital for the regional-global ecology. In 2003, the TPRR was listed as a World Heritage Site for its outstanding biodiversity, geology, landscape, and rare and endangered species (United Nations Educational Scientific and Cultural Organization (UNESCO), 2003). In 2010, the UNESCO World Heritage Center adopted a minor modification to the TPRR’s boundaries (Yunnan Province, 2012).

There are fifteen PAs in the TPRR, including different levels of nature reserves and parks (Table 1). One of the PAs, the Gaoligongshan National Nature Reserve, is divided into three parts (northern, middle, and southern subregions) as three PAs in our study based on geographical location and climate; these parts are managed by different districts and counties. Notably, we excluded wetland PAs, such as the Lashihai Plateau Wetland Provincial Nature Reserve and Qinghuadian National Wetland Park. Thus, in this study, we analyzed forest changes in 14 PAs.

2.2 Methods

2.2.1 Calculation of forest area in TPRR

In this calculation, we used the 30 m annual land cover dataset in China, the first Landsat-derived CLCD produced by the Google Earth Engine, with 79.31% overall accuracy and 85.49% accuracy for the forest category (Yang and Huang, 2021). The classification system for this dataset includes nine major land covers, which are cropland, forest, shrub, grassland, water, snow and ice, barren,

TABLE 1 List of all protected areas in the Three Parallel Rivers Region and their year of establishment.

No.	Name of Protected Area	Type	Level	Established year
1	Gaoligongshan National Nature Reserve	Nature Reserve	National	1983
2	Baima Snow Mountain National Nature Reserve	Nature Reserve	National	1983
3	Yunlong Tianchi National Nature Reserve	Nature Reserve	National	1983
4	Yulong Snow Mountain Nature Reserve	Nature Reserve	Provincial	1984
5	Habaxueshan Nature Reserve	Nature Reserve	Provincial	1984
6	Bitahai Nature Reserve	Nature Reserve	Provincial	1984
7	Napahai Nature Reserve	Nature Reserve	Provincial	1984
8	Lashihai Nature Reserve	Nature Reserve	Provincial	1998
9	Lanping Yunling Provincial Nature Reserve	Nature Reserve	Provincial	2006
10	Cuipingshan County Nature Reserve	Nature Reserve	County	2003
11	Mt.Yulong Snow-Glacier-Geological Park	Natural Park	National	1998
12	Feilai Temple National Forest Park	Natural Park	National	2000
13	Xinshengqiao National Forest Park	Natural Park	National	2001
14	Yulong Liming-Laojunshan National Geopark	Natural Park	National	2004
15	Qinghuadian National Wetland Park	Natural Park	National	2016

impervious, and wetland. Forests include wooded land (>30% cover), open woodland, and tracks, excluding new young woodland and forest belts that are not recognizable from remote sensing imagery (Liu et al., 2003, Liu et al., 2018). We extracted forest area data from the CLCD in the TPRR for 20 consecutive years (2000–2020). We also calculated the forest area of all PAs for each year from 2000 to 2020 by overlaying the vector boundary of all PAs with the forest cover layer from the CLCD. All related spatial analyses were performed using ArcGIS 10.6. Next, we fitted a linear regression to the relationship between time on the x-axis and forest area on the y-axis. According to the results of the linear regression, the trend of the mean forest area (2000–2020) of each PA (FAtrend) was increasing ($P<0.05$), steady ($P>0.05$), and decreasing ($P<0.05$).

2.2.2 Assessing each PA's state and relative change in forest area

For this study area, we selected areas inside and outside the PAs as the treated and control sites. We created 1 km^2 grids of the entire TPRR and assigned the grids inside and outside PAs with values of 1 and 0, respectively. We used propensity score matching (PSM) to eliminate the influence of differences in environmental factors on the sites, 6195 pairs of sites were matched. PSM is a matching method that calculates the propensity score, which is the conditional probability of assignment to a particular treatment given a vector of observed covariates, to control for bias and achieve equalization (Rosenbaum and Rubin, 1983). Here, based on major geographic and anthropogenic factors that may have an impact on matching, five control variables were considered covariates: elevation, slope, soil, distance to the nearest road, and distance to the nearest settlement. We calculated the values of these five variables at the treated and control sites in ArcGIS 10.6 by using Zonal Statistics, and completed the matching. PSM was accomplished in R version 4.3.0 with the 'MatchIt' package, the 'nearest' method was selected, and the caliper value was set to 0.2 (Cuenca et al., 2016). Therefore, the control sites outside the PAs could be counterfactual areas of the PAs, as matched unprotected areas, because there are no unprotected blank control samples of the same time period (Ferraro, 2009). Owing to the large north-south span of the TPRR, we selected control sites within a 10–50 km buffer region around each PA to avoid the spillover effect of PAs on their unprotected adjacent surroundings (Fuller et al., 2019) and removed grids that were overlaid by other PAs or their 0–10 km buffer regions.

We calculated the forest area of the treated and control sites in ArcGIS 10.6 by using Zonal Statistics from 2000 to 2020. For each PA, we compared the differences in the mean forest area for each year between the treated grids inside each PA and their matched control grids to test the state of the PA (FAstate). Because the forest areas as the dependent variable are correlated, we chose a mixed linear model (tested using "lme4" in R) to compare the differences of matched samples for each PAs. We chose mixed linear model because this model does not require a normal distribution as well as independence between samples, and also takes into account the correlation between years and groups. We set forest area as the response variable, inside and outside sample groups as fixed effects, and year as a random effect. According to the results of linear mixed model, PAs were in a good state when the mean value of the forest area of the treated grids was significantly higher than that of the matched control grids ($P<0.05$); in a moderate state when the mean value of the forest area of the treated grids showed no significant difference compared with that of the matched control grids ($P>0.05$); and in a bad state when the mean value of the forest area of the treated grids was significantly lower than that of the matched control grids ($P<0.05$).

For the relative change in each PA (FAchange), we compared the difference in the mean value of the slope of forest changes (2000–2020) between the treated grids inside each PA and their matched control grids. According to the Wilcoxon signed ranks test in R version 4.3.0, those PAs were increasing when the slope of forest changes in treated grids was significantly higher than that of the matched control grids ($P<0.05$); relatively steady when the slope of forest changes in treated grids showed no significant difference compared with that of the matched control grids ($P>0.05$); and decreasing when the slope of the forest changes in the treated grids was significantly lower than that of the matched control grids ($P<0.05$).

2.2.3 Framework of conservation effectiveness assessment by integrating the state, trend, and relative change in the forest area of PAs

We developed a comprehensive framework by integrating the status, trends, and relative changes in the forest area of natural reserves, aiming to explore the assessment of natural reserve effectiveness in protecting forest ecosystems (Figure 1). This framework consists of three primary steps, each entailing distinct assessments that could impact the final outcome. Initially, the first step entails categorizing the baseline conditions of natural reserves into three distinct states (i.e., good, moderate, and bad) (Figure 1A). Subsequently, the second step involves determining the trajectory of natural reserves under various conditions (i.e., increasing, steady, and decreasing), resulting in nine possible scenarios (see Figure 1B). Lastly, the third step entails categorizing the outcomes of relative changes based on the situations identified in the preceding steps. Each gray arrow in the figure denotes the test results of relative changes corresponding to their respective categories, resulting in a total of 27 scenarios (see Figure 1C). In summary, each step entails the categorization of test results.

Our framework differs from previous studies in two ways. When PAs with good states showed an increasing or steady trend, they were considered to have positive impacts, regardless of the relative changes found. When PAs with bad states showed a decreasing or steady trend, they were considered to have negative impacts, regardless of the relative changes found. The remaining PAs in other situations were considered to have positive, nonsignificant, or negative impacts according to commonly used methods in the literature (Ren et al., 2015; Bowker et al., 2017; Liu et al., 2022): PAs with relative increasing forest areas had positive impacts, PAs with relatively steady forest changes had nonsignificant impacts, and PAs with relative decreasing forest areas had negative impacts (Figure 1C).

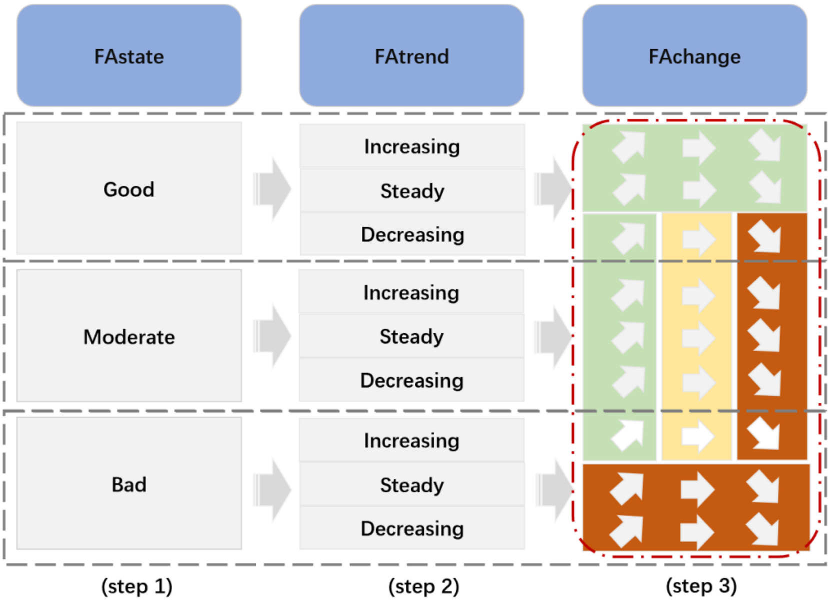

FIGURE 1
The framework of conservation effectiveness assessment by integrating the state, trend, and relative change in forest area of PAs. FAstate refers to the state of the forest area; FAtrend refers to the forest trend; FAchange refers to the relative change in the forest area. Step 1 divides the states into three types: good, moderate, and bad. Step 2 identifies the trend of PAs: increasing, steady, and decreasing. Step 3 explores conservation effectiveness by making judgments according to the relative change in PAs in different situations. Inside the dotted red border, the three types of gray arrows represent the results of relative change, the upward arrow represents a relative increasing change, horizontal arrows represent a relative steady change, and downward arrows represent a relative decreasing change. The three colors of the background denote the results of the conservation effectiveness situation: green, positive; orange, nonsignificant; and red, negative.

2.2.4 Analysis of factors affecting states and relative changes

To explore possible factors influencing the conservation effectiveness of PAs and the extent of their influence, the state and relative changes in PAs were treated as independent variables. We take the 6,195 treated samples inside PAs from the previous matched samples as objects. Then we assigned the dependent variable a value of 1 for positively significant, 0 for non-significant, and -1 for negatively significant, based on the results of the tests for each PA in terms of state and relative change, separately. We selected several factors affecting the states and relative changes from natural factors, human interference, and management levels as dependent variables Natural factors included elevation, slope, mean annual temperature, and total annual precipitation. Human interference included the distance to the nearest road, change in distance to the nearest road, initial population density (2000), and changes in population density. Management level was a categorical variable with ranks of 1 (national nature reserves), 2 (provincial- and county-level nature reserves), and

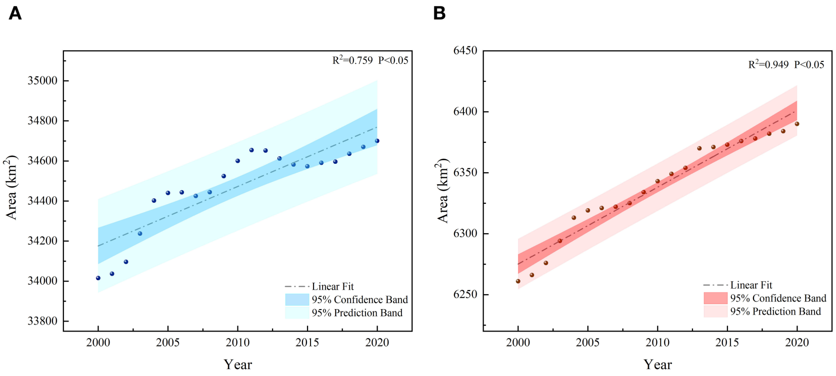

FIGURE 2
(A) Changes in forest area in TPRR, 2000–2020. **(B)** Changes in forest area in PAs, 2000–2020.

3 (national natural parks). We then used the random forest regression model in R version 4.3.0 to identify the major factors (Cao et al., 2021). The percentage increase in the mean squared error was used to compare the importance of these factors. Partial dependence analyses were used to identify the relationships between major and independent variables.

3 Results

3.1 Changes and trends in forest areas

For the entire region of the TPRR, the total area of the forest ecosystem was 34,700 km^2 in 2020, and forest coverage was 76.8%.

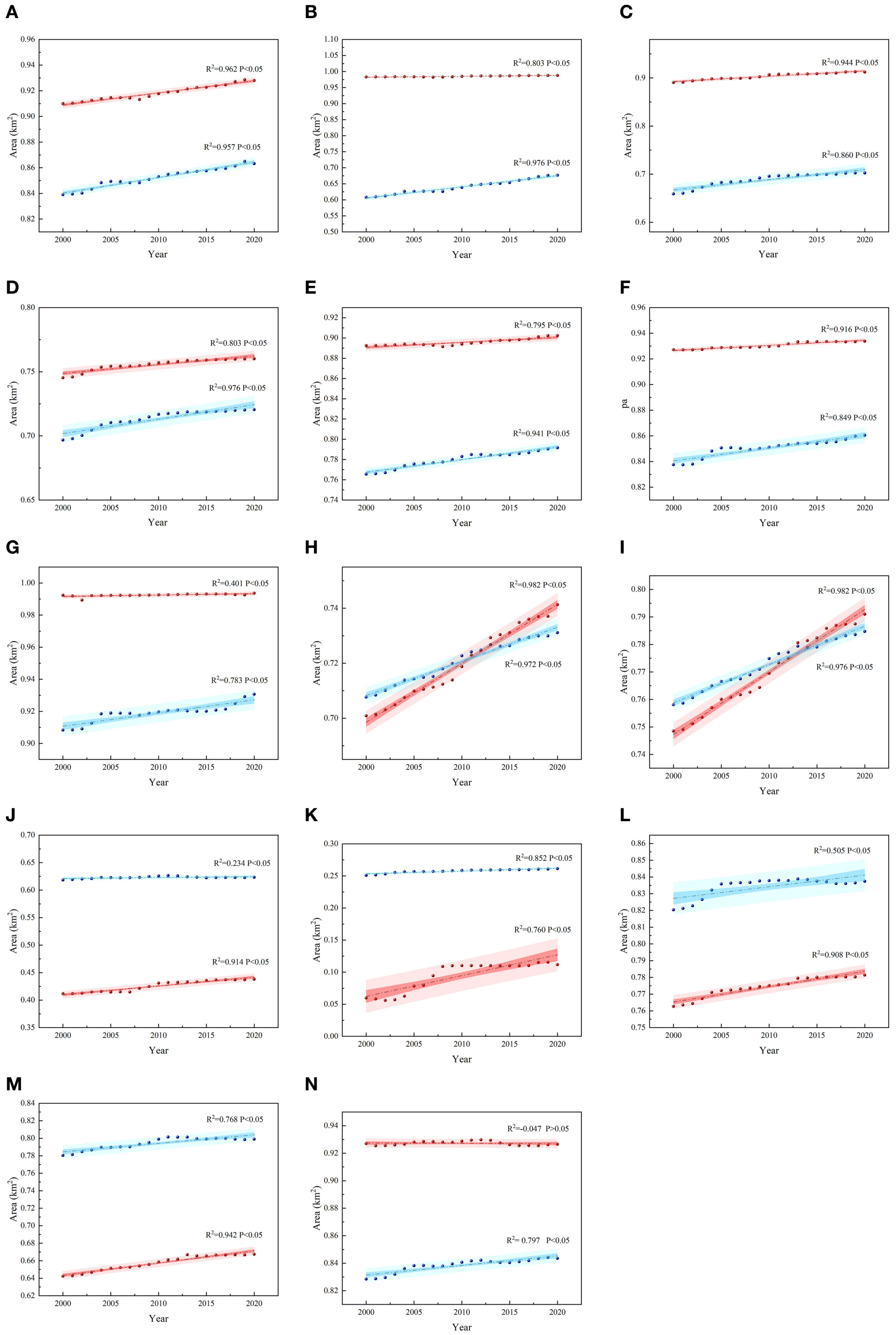

FIGURE 3
Average area of forest in matched treated grids of PAs and matched control grids of the outside, 2000–2020. **(A)** Cuipingshan County Nature Reserve; **(B)** Xinshengqiao National Forest Park; **(C)** Bitahai Nature Reserve; **(D)** Baima Snow Mountain National Nature Resrve; **(E)** Lanping Yunling Provincial Nature Reserve; **(F)** Middle Section of Gaoligongshan National Nature Reserve; **(G)** Southern Section of Gaoligongshan National Nature Reserve; **(H)** Mt.Yulong Snow-Glacier-Geological Park; **(I)** Yulong Snow Mountain Nature Reserve; **(J)** Feilai Temple National Forest Park; **(K)** Napahai Nature Reserve; **(L)** Northern Section of Gaoligongshan National Nature Reserve; **(M)** Habaxueshan Nature Reserve; **(N)** Yulong Liming-Laojunshan National Geopark. Red points refer to matched treated grids in each PA; blue points refer to matched control grids outside each PA.

From 2000 to 2020, this trend showed a significant increase (R^2 = 0.753, $P<0.05$) (Figure 2A) of 2%. During the first seven years (2000–2006), the forest area showed substantial growth and reached its first peak in 2006. The growth trends fluctuated. From 2015 to 2020, the forest area resumed a steady growth trend.

For all PAs in the TPRR, changes in forest area also showed a significant increase (R^2 = 0.919, $P<0.05$) (Figure 2B). By the end of 2020, the forest area was 6,390 km^2 in the PAs, a 2% increase from 2000. There was a large increase from 2000 to 2006 in all PAs, similar to the trends observed in the entire region. However, in contrast with the TPRR, the growth trends of the forest area from 2007 to 2012 were close to the fitted curve. After 2012, the magnitude of change in forest area in PAs gradually increased. Most PAs (n=13) in the TPRR have shown significant increasing trends over the past 20 years, (Figures 3A–M) except for the Yulong Liming-Laojunshan National Geopark, which had a stable tendency (Figure 3N).

3.2 State and relative change in each PA's forest

The results of the Wilcoxon tests indicated that of the forest ecosystems of the fourteen PAs, eight were in a good state, where the mean values of the forest area of the treated grids were significantly higher than those of the matched control grids ($P<0.05$) over the past 20 years; one was in a moderate state; and five were in a bad state. For relative changes in forest areas, of the fourteen PAs, four PAs showed a relative increase in the slope of forest changes in their treated grids, which was significantly higher than that of the matched control grids ($P<0.05$); four PAs showed relatively nonsignificant changes, and 6 PAs showed relatively decreasing trends from 2000 to 2020 (Table 2). According to the framework of conservation effectiveness assessment, by integrating the state, trend, and relative change in the PAs' forest areas (Figure 1), of the fourteen PAs, we identified twelve PAs with positive effects and two PAs with nonsignificant effects (Figure 4).

3.3 Major factors

All PAs (n=13) except for one that showed a steady trend showed significant increasing trends. Notably, we only identified the major factors affecting the states and relative changes in PAs.

3.3.1 Major factors affecting the states of PAs

Random forest regression analysis showed that all independent variables were relevant factors affecting the state of the forest, with an explanatory rate of 96.09% (Figure 5A). Among the nine factors, annual total precipitation was the most important. The partial dependence plots showed that the forest ecosystems of PAs were maintained in the best state when the annual total precipitation ranged from 600 to 700 mm and from 1100 to 1200 mm (Figure 5B). The distance to the nearest road was the most important factor, and the best range should be from 0 to 20 km to maintain a good state in PAs (Figure 5C). Change in distance to the nearest roads was the third most important factor, and PAs' forests were in a good state when they were close to zero (Figure 5D). Notably, the results also showed that management level was an important factor for the dependent variable, which indicated that national PAs (nature reserves and natural parks) were in a better state than local (provincial- and county-level) nature reserves (Figure 5E). The remaining independent variables also contribute to some extent (Figures 5F–J).

3.3.2 Major factors affecting relative changes in PAs

Random forest regression analysis showed that all parameters were important factors affecting the relative change in the forest areas of PAs, with an explanatory rate of 95.19% (Figure 6A). Similar to the factors affecting the state of PAs' forests, annual total precipitation was the most important factor. The partial dependence plots showed that the relative changes in forest areas of PAs increased when the annual total precipitation increased from 600 to 1000 mm and kept in relative steady when the annual total precipitation was higher than

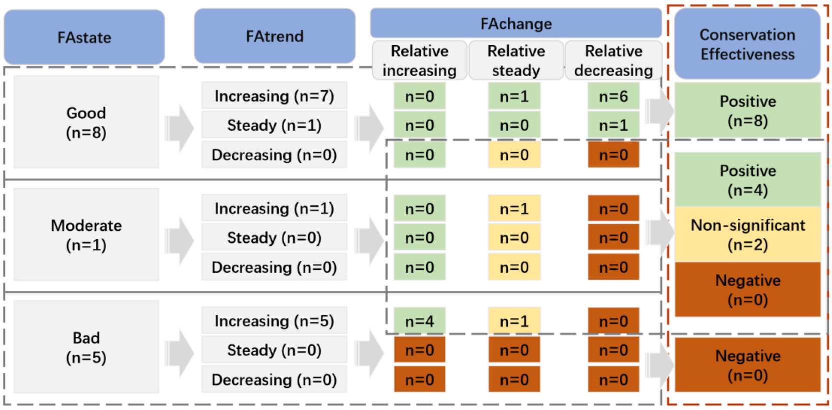

FIGURE 4
Results of judgments under the framework of conservation effectiveness assessment by integrating the state, trend, and relative change in forest area of PAs in TPRR. FAstate refers to the state of the forest area; FAtrend refers to the trend of the forest trend; FAchange refers to the relative change in the forest area. The results of the conservation effectiveness were summarized by the classifications of FAstate, FAtrend, and FAchange. The three colors of the background denote the results of the conservation effectiveness situation: green, positive; orange, nonsignificant; and red, negative.

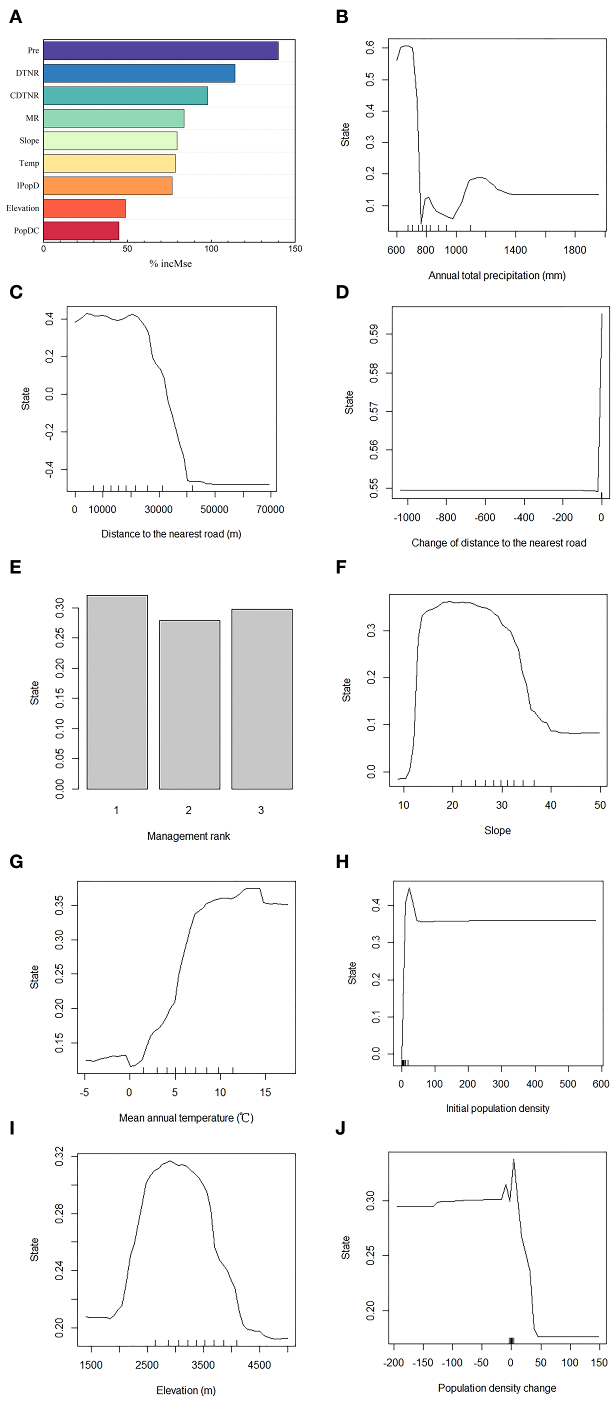

FIGURE 5
(A) The main factors influencing the state indicators of PAs in the random forest model are denoted by the percentage increase in the mean squared error (%IncMSE). Pre: Annual total precipation; DTNR: Distance to the nearest road; CDTNR: Change in the distance to the nearest road; MR: Management rank; Temp: Annual mean temperature; IPopD: Initial population density; PopDC: population density change. **(B–J)** Response functions of state. Each panel shows the response of a conservation effectiveness indicator across a single variable while holding the other variables constant. Change in distance to the road is expressed as the rate of change in distance to the road from 2000 to 2020. For management rank, 1 denotes the national nature reserves, 2 denotes local nature reserves, and 3 denotes the national natural park.

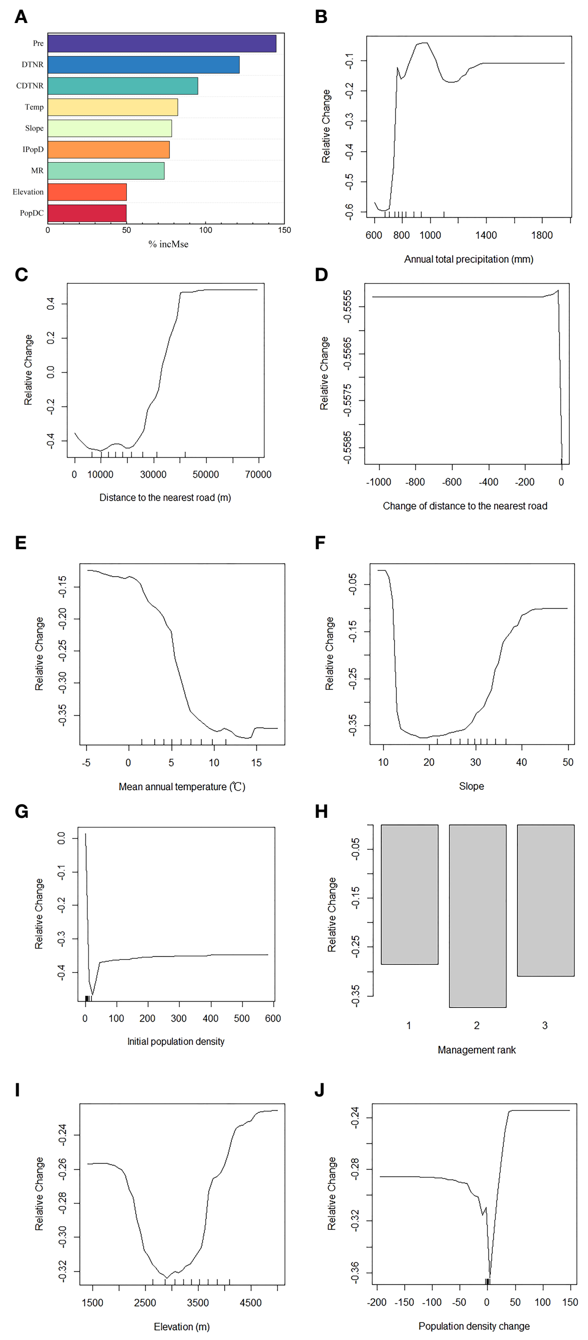

FIGURE 6
(A) The main factors influencing the change indicators of PAs in the random forest model denoted by the percentage increase in the mean squared error (%IncMSE). Pre: Annual total precipation; DTNR: Distance to the nearest road; CDTNR: Change in the distance to the nearest road; MR: Management rank; Temp: Annual mean temperature; IPopD: Initial population density; PopDC: population density change. **(B–J)** Response functions of relative change. Each panel shows the response of a conservation effectiveness indicator across a single variable while holding the other variables constant. Change in distance to the road is expressed as the rate of change in distance to the road from 2000 to 2020. For management rank, 1 denotes the national nature reserves, 2 denotes the local nature reserves, and 3 denotes the national natural park.

TABLE 2 Linear mixed model test results for state and the Wilcoxon signed ranks test results for relative change.

No.	Name of Protected Area	S-t	S-p	RC-al	RC-p
1	North of Gaoligongshan National Nature Reserve	**93.2**	**P<0.001*** **	**higher**	**P<0.01** **
2	Middle of Gaoligongshan National Nature Reserve	**−79.83**	**P<0.001*** **	**lower**	**P<0.001*** **
3	South of Gaoligongshan National Nature Reserve	**−64.19**	**P<0.001*** **	**lower**	**P<0.001*** **
4	Baima Snow Mountain National Nature Reserve	**−62.88**	**P<0.001*** **	**lower**	**P<0.001*** **
5	Yulong Snow Mountain Nature Reserve	**2.217**	**P<0.05* **	**higher**	**P<0.05* **
6	Habaxueshan Nature Reserve	**193.2**	**P<0.001*** **	**ns**	**P>0.05**
7	Bitahai Nature Reserve	**−133.7**	**P<0.001*** **	**lower**	**P<0.01** **
8	Napahai Nature Reserve	**36.674**	**P<0.001*** **	**higher**	**P<0.05* **
9	Lanping Yunling Provincial Nature Reserve	**−94.79**	**P<0.001*** **	**lower**	**P<0.001*** **
10	Cuipingshan County Nature Reserve	**−129.5**	**P<0.001*** **	**ns**	**P>0.05**
11	Mt.Yulong Snow-Glacier-Geological Park	**0.544**	**P>0.05**	**ns**	**P>0.05**
12	Feilai Temple National Forest Park	**97.45**	**P<0.001*** **	**higher**	**P<0.05* **
13	Xinshengqiao National Forest Park	**−78.65**	**P<0.001*** **	**ns**	**P>0.05**
14	Yulong Liming-Laojunshan National Geopark	**−87.58**	**P<0.001*** **	**lower**	**P<0.001*** **

S-t is the t-value of the Linear mixed model test, t<0 means that the treated sample is better than the matched samples, t>0 means that the matched sample is better than the treated samples, and s-p is the p-value of the test.

RC-al is the alternative hypothesis for relative change in the Wilcoxon test, "higher" means that the treated sample is higher than the matched samples, "ns" means that that the treated sample has no significant difference compared with the matched sample, "lower" means that the treated sample is lower than the matched samples, and RC-p is the p-value of the test.

"*" means significant at the 0.05 level, "**" means significant at the 0.01 level, "***" means significant at the 0.001 level.

1000 mm (Figure 6B). The distance to the nearest road was the second most important factor, and the relative changes in forest areas of PAs increased when the distance to the nearest road increased from 20 to 40 km and remained in relative steady when the distance to the nearest road was greater than 40 km (Figure 6C). The change in distance to the nearest roads was the third most important factor, and PAs' forests were relatively decreasing when it close to 0 (Figure 6D). PAs' forests showed a relatively decreasing trend when the mean annual temperature increased from 0 to 15°C (Figure 6E). Our results showed that management level had less impact on the dependent variable (Figure 5E). The remaining independent variables also contribute to some extent (Figures 6F–J).

4 Discussion

This study constructed a framework for assessing conservation effectiveness by classifying the results of the state, trend, and relative change in forest areas in PAs by a three-step process. Other studies have assessed the effectiveness of conservation based on relative changes in one or more indicators (Jones et al., 2018; Young et al., 2020; Graham et al., 2021; Zheng et al., 2021). This study also integrated three dimensions from the perspective of time to avoid misjudging conservation effectiveness. Because of the stabilization of forests' ecosystems after the climax community (Huo et al., 2012; Zhang et al., 2018), when PAs are in a good state (better than the matched unprotected areas) and show increasing or steady trends during the study period, they could be considered to have positive effects in protecting forests regardless of the relative changes found. By contrast, merely comparing deforestation rates within PAs with rates in matched unprotected areas to represent conservation effectiveness may ignore the steady situation and underestimate some positive results (Wolf et al., 2021). Our results revealed that 12 (86%) of the PAs had a positive effect, and two had a nonsignificant effect. Among these twelve PAs, the 50% (n=7) with a relative decrease would be considered to have a negative effect according to the traditional method. Notably, if, in this study, we only assessed the conservation effectiveness according to the results of relative change, as performed in the literature, our conclusion would be misjudged (Wade et al., 2020; Rahman and Islam, 2021). Our methods avoid underestimation and facilitate suitable judgment specifically aimed at PAs that may achieve a climax community.

Overall, forest area in the TPRR and all the PAs showed a volatile increase since 2000, revealing a generally increasing trend that may be closely related to obtaining membership in the World Nature Heritage Site in 2003 (United Nations Educational Scientific and Cultural Organization (UNESCO), 2003). Except the rapid growth in 2003, another peak was probably associated with the minor boundary modification inscribed in 2010 that acquired approval from the State Council in 2012 (Yunnan Province, 2012), which stimulated the conservation of the entire region. Studies have also confirmed that policy changes were able to be attributed to a series of factors affecting forest area change dynamics (Feng et al., 2021), and changes in the surrounding landscape affect biodiversity and ecosystem functions (Marques et al., 2022), indicating that a holistic protection policy on a regional scale, particularly in biodiversity hotspots, is essential and effective.

The analysis of potential factors that affect PAs' conservation effectiveness demonstrated that annual total precipitation was the most important factor for the dependent variables of state and relative change. PAs with annual total precipitation from 600 to 700 mm and higher than 1000 mm were additionally likely to be in a good state and have a relatively increasing trend, that is, a positive effect. Temperature is also a major factor in PAs' conservation effectiveness and is the most important factor affecting vegetation growth (Pan et al., 2015; Li et al., 2020). However, from 10 to 15°C, annual temperature showed different impacts on the states and relative changes in PAs. The reason for these differences may be the variation in topography and elevation among PAs, where growing reasons vary (e.g., high elevation in the Baima Snow Mountain National Nature Reserve and low mountain areas in Xinshengqiao National Forest Park). Studies have also shown that meteorological factors, such as precipitation and temperature, are major factors affecting the effectiveness of PAs in maintaining ecosystem services (Cao et al., 2021).

Human impacts, such as road construction and management, also play influential roles in PAs' conservation effectiveness to some extent. Regarding distance to the nearest road, different impacts were found on the states and relative changes in PAs. PAs 0–20 km from the nearest road were more likely to be in a good state, and PAs 20–40 km from the nearest road were more likely to show a relatively increasing trend. Thus, surrounding roads are conducive to the state of PAs' forests within a certain range because roads within or near PAs might facilitate patrolling. It has also been shown that species richness increases with elevation and distance from the edge of the protected area, and that species assemblage categories differ by distance, supporting the differences in the impact of roads on conservation effectiveness (Ji et al., 2022). That deforestation declined as the distance from the road increased (Barber et al., 2014; Milien et al., 2021) illustrates that the relative change in PAs' forest areas would be higher when the distance to the nearest road was longer than 40 km. At the management level, nature reserves are commonly assumed to be lands with higher levels of protection and management compared to natural park. However, the states of local (provincial- and county-level) nature reserves performed worse than national natural parks. This finding may be similar to that in the literature that the threat level of national PAs is lower than that of local PAs in the TPRR (Ye et al., 2015). We suggest that local administration departments focus on the threats of provincial- and county-level nature reserves and enhance improvement initiatives. Therefore, the overall conservation of World Heritage Sites is promoted by this type of effectiveness assessment (Allan et al., 2017).

5 Conclusion

In this study, we established a framework through a series of judgments according to the states, trends, and relative changes in PAs' forested areas. A case study of the TPPR implied that the framework would be more useful in regions with high biodiversity and steady ecosystems. This framework can better avoid underestimation in conservation effectiveness assessment tasks than traditional methods can. Thus, we posit that this framework is suitable for future global or country-level assessments.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

HS: Conceptualization, Formal analysis, Methodology, Writing – original draft. CF: Methodology, Software, Writing – original draft. JT: Methodology, Software, Writing – original draft. LF: Methodology, Software, Writing – original draft. MC: Methodology, Software, Writing – original draft. WW: Funding acquisition, Methodology, Project administration, Writing – review & editing.

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Conflict of interest

Author LF is employed by Zhengzhou University Environmental Technology Consulting Engineering Co., Ltd.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1321974/full#supplementary-material

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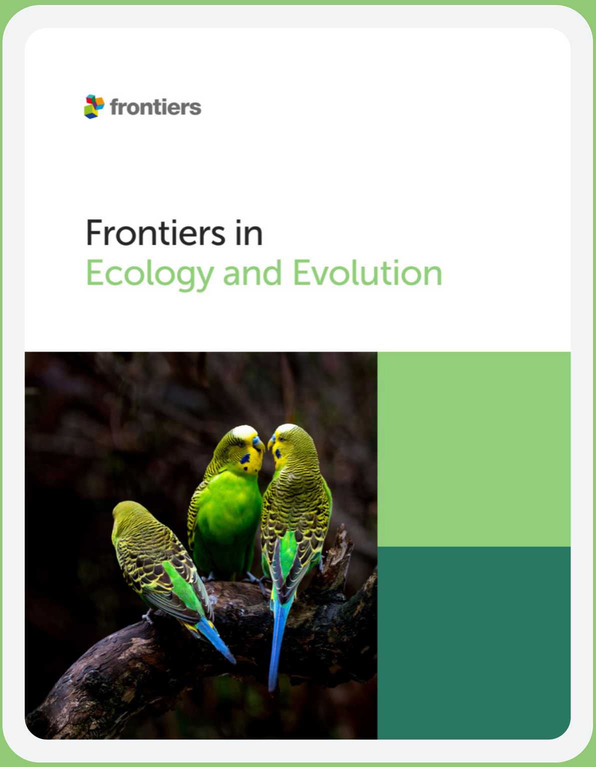

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