Research Topics

Global change ecology: threats and solutions

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and Vincent Resh

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Global change ecology: threats and solutions

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Editorial: Global change ecology: threats and solutions

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Editorial on the Research Topic
Global change ecology: threats and solutions

1 Introduction

The special Research Topic, "Global Change Ecology: Threats and Solutions," seeks to illuminate the complex interplay between global environmental changes and ecological systems. In an era defined by rapid transformations driven by human activities and natural processes—such as climate change, urbanization, biological invasions, and pollution—an understanding of these dynamics is crucial. These global changes are causing significant biodiversity loss and triggering adverse eco-evolutionary impacts at various scales, from individual populations to entire ecosystems. Thus, our Research Topic of interdisciplinary articles provides crucial insights into how such environmental shifts can reshape biodiversity and ecosystem functions.

This topic encompasses a wide array of studies focusing on the effects of environmental stresses on diverse biotic communities, ranging from terrestrial to marine ecosystems. By integrating experimental, modeled, and observed data, the contributions explore ecological and evolutionary responses that enhance our ability to forecast and mitigate the impacts of environmental disturbances. Articles in this Research Topic address key areas such as ecological responses to climate variability, land use dynamics, sustainable agricultural practices, urban environmental influences, and the ecological ramifications of pollutants and invasive species. Through such comprehensive scrutiny, the research presented aims not only to document current changes but also to foster resilience and resistance within ecosystems, thereby aiding in the development of sustainable environmental policies and practices for the Anthropocene.

2 Major contributions

Our Research Topic brings together a diverse array of studies that delve deep into the dynamic interactions between global environmental changes and ecological systems. In their exploration of aquatic protected areas (i.e., on the Qinghai-Tibet Plateau in China), Li et al. highlight the strategic establishment and location of these areas and the significant conservation gaps that they attempt to fill, underscoring the need for enhanced community-based conservation practices and increased research funding to protect threatened species. Similarly, the study by Doloiras-Laraño et al. examines how alterations in river flow affect microbial communities in hyporheic zones, and thereby demonstrates that changes in water discharge can significantly influence microbial diversity and ecosystem services such as nutrient cycling and pollutant degradation. This research points to the critical need for managing river flow regimes to sustain the ecological integrity of these vital zones. Further addressing the challenge of invasive species, Mu and Li use species distribution models to evaluate the risk posed by *Chelydra serpentina* in China. Their findings indicate a potential expansion of the species' habitat, which can heighten risks to local biodiversity. They also stress the importance of advanced monitoring techniques (i.e., with environmental DNA) for effective management. In the realm of biodiversity and ecosystem management, studies by Zhang et al., Chen et al., and Li et al. collectively address the impacts of global changes on species distributions and agricultural practices.

These studies show that strategic, adaptive management approaches can significantly influence biodiversity conservation, from optimizing species distributions under changing climates to enhancing arthropod diversity in rice agroecosystems through sustainable practices. Contributions that further our understanding of ecological dynamics, Yang et al. investigate how variations in precipitation affect nutrient dynamics and microbial activity in agroecosystem subsoils, emphasizing the importance of adaptive soil management strategies in response to climate variability. Additionally, Cambrone et al. apply random forest models to set global conservation priorities for the pigeons and doves of the family Columbidae, thus showcasing the usefulness of data-driven approaches to refining conservation efforts. Lastly, the opinion piece by Li et al. critiques current biodiversity modeling techniques and advocates for incorporating moderators into dissimilarity-based models, proposing a more sophisticated approach to predicting ecological changes. Their call for enhanced modeling accuracy underscores the ongoing need for innovation in ecological research methodologies.

Together, these studies illuminate the multifaceted approaches necessary to understand and combat the ecological impacts of global changes. They not only deepen our understanding of ecological systems but also showcase the effectiveness of interdisciplinary approaches in advancing conservation strategies and sustainable management practices across different ecological contexts.

3 Impact of research and conclusion

As the challenges posed by global ecological changes escalate, the need for a collaborative and integrated research approach becomes more evident. Consequently, our Research Topic profoundly enhances our comprehension of ecological responses to global changes. This Research Topic spans diverse ecosystems and biological scales, illustrating the intricate interplay between human-induced pressures (e.g., climate change, urbanization, and biological invasions) and natural ecological dynamics. The findings from these studies are pivotal in advocating for and developing multidisciplinary approaches that blend cutting-edge scientific methodologies with practical conservation strategies. By doing so, they not only deepen our understanding of the ecological impacts of human activities and natural processes but also showcase effective strategies to enhance ecosystem resilience. For instance, the predictive models and conservation strategies highlighted throughout offer practical tools for forecasting and mitigating the impacts of environmental disturbances, which are crucial for policy-making and ecological management. This paradigm is essential for developing effective, sustainable responses that support the coexistence of human and natural systems in the Anthropocene.

Author contributions

J-RL: Writing–original draft, Writing–review and editing. QC: Writing–review and editing. KW: Writing–review and editing. M-CC: Writing–original draft, Writing–review and editing. VR: Writing - original draft, 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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Stronger microbial nutrient limitations in subsoil along the precipitation gradient of agroecosystem: insights from soil enzyme activity and stoichiometry

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Introduction: Soil extracellular enzymes are central in terrestrial ecosystem responses to climate change, and their research can be crucial for assessing microbial nutrient demand. However, the effects of climate-induced precipitation patterns on soil microbial nutrient demand in different soil profiles of agroecosystems are rarely studied.

Methods: Here, we present how the precipitation gradient affects soil enzymes related to carbon (C), nitrogen (N) and phosphorus (P) cycling and identified microbial nutrient limitation determinants at five depth intervals (0–10, 10–20, 20–30, 30–40, and 40–50 cm) in seven agroecosystems.

Results and Discussion: We found that N- and P-acquiring enzymes have a tendency to decrease or increase, respectively, but C-acquiring enzymes did not change along the precipitation gradient throughout soil profiles. Soil pH and moisture were the most important factors affecting the enzyme activity in 0–50 cm. Our results also revealed a crucial soil boundary (at 20 cm) that differentiated responses of microbial nutrient limitation to precipitation changes. In the topsoil (0–20 cm), the stoichiometry of soil nutrients did not vary with precipitation. Microbial P limitation was exacerbated with increased precipitation, which was controlled by soil pH and moisture in the topsoil. In contrast, in the subsoil (20–50 cm), soil nutrient stoichiometry decreased with increasing precipitation, and microbial C and P limitation displayed a positive correlation with precipitation. Furthermore, microbial P limitation tended to be stronger in the subsoil than in the topsoil along the precipitation gradient. Microbial C and P limitation was regulated by the soil nutrients and their stoichiometry in the subsoil. Our study is an essential step in soil enzyme activity and stoichiometry response to precipitation in agroecosystems and provides novel insights into understanding microbial nutrient limitation mechanisms in soil profiles along the precipitation gradient.

KEYWORDS

cropland, ecological stoichiometry, extracellular enzyme, nutrient limitation, Northeast China transect

1. Introduction

Changes in precipitation can lead to shifts in belowground ecological processes that are interlinked with primary production, damaging regional crop production in agroecosystems (Lesk et al., 2016; Franco et al., 2019; Sünnemann et al., 2021). Under rapid precipitation changes, carbon (C), nitrogen (N), and phosphorus (P) cycles may become uncoupled because of the different degrees of control exerted on the supply of these elements by biological and geochemical processes (Delgado-Baquerizo et al., 2013). To meet the food demand, farmers are continuously raising N and P inputs, altering C availability, and leading to a further imbalance in the stoichiometry of microbial substrates in soils (Peñuelas et al., 2013; Schleuss et al., 2021). A combination of precipitation and agricultural activities more drastically alters the patterns, magnitude, and extent of nutrient limitation in soil (Marklein and Houlton, 2012). Such limitation is directly relevant to the fate of soil microbial processes (Camenzind et al., 2018), but the extent and nature of microbial nutrient limitation has never been systematically assessed in agroecosystems along a precipitation gradient. Thus, the underlying ecological mechanisms governing microbial nutrient limitation in agroecosystems are required to support future predictions of precipitation changes.

Ecological stoichiometry and ionomics provide a research framework to facilitate improved mitigation and forecasting of the effects of changing precipitation patterns (Graham and Hofmockel, 2022). Ionomics may link ecological phenomena to the nutritional needs of organisms and responses to environmental stressors (Kaspari, 2021). Ecological stoichiometry takes into account the balance between the nutrient demand of organisms and the nutrient supply in their habitats, their interactions with abiotic and biotic factors and nutrient cycling of ecosystems (Filipiak and Filipiak, 2022). Nutrient availability, especially N and P, impacts microbial respiration and growth because microorganisms need to maintain a homeostasis composition of C and nutrients (Manzoni et al., 2012). Ecological stoichiometry could mediate the function of brown food webs and microbial nutrient metabolism by reallocating resources to extracellular enzymes (Zhang et al., 2019).

Extracellular enzyme activities (EEA) play a central role in regulating imbalances between resources and growth demands in microbe self-organizational processes (Sinsabaugh and Follstad Shah, 2011; Sinsabaugh et al., 2015). Extracellular enzymes are mediators of decomposition and mineralization of N and P (Schimel and Weintraub, 2003; Moorhead and Sinsabaugh, 2006), and are also indicators of microbial nutrient demand (Moorhead et al., 2016). According to resource allocation theory, when a resource is scarce, microorganisms preferentially invest metabolic resources into extracellular enzyme production to maximize the use of the limited element (Allison and Vitousek, 2005; Johnson et al., 2010; Mooshammer et al., 2014). Due to the context dependence of enzyme activity, EEA has gradually received greater attention and become a popular method for examining the direct effects of precipitation on the functional potential of the soil microbial community in field experiments (Weedon et al., 2011; Henry, 2013).

The theory of enzyme stoichiometry further reflects the balance between microbial nutrient demand and soil nutrient resource supplies, highlighting the limiting factors of biogeochemical cycling in terrestrial ecosystems (Sinsabaugh et al., 2009; Zechmeister-Boltenstern et al., 2015; Xu et al., 2017). Sinsabaugh et al. (2008) developed an approach to visualize the relative C, N, and P controls on soil microbial communities by plotting the ratios of activities for enzymes associated with C, N and P acquisition. Moorhead et al. (2016) proposed that vector lengths and angles can be used to improve the quantification and visualization of these controls. A global meta-analysis exhibited that enzymatic C:P and N:P ratios were inversely related to precipitation, while the ratio of C:N acquisition increased with precipitation (Sinsabaugh et al., 2008). In forest ecosystems, the C:N, C:P, and N:P acquisition ratios were negatively related to precipitation from a depth of 0–10 cm soil (Xu et al., 2017). However, Cui et al. (2019a) found a shift from P to N limitation of microorganisms with an increase in precipitation from 300 mm to 900 mm in grassland ecosystems from the 0–20 cm soil layer. Therefore, generalizing the effects of precipitation on soil EEA can be challenging and elusive, and it is necessary to strengthen our research on EEA patterns at regional scales. To the best of our knowledge, there remains a lack of studies on the impact of precipitation gradients on soil enzyme in agroecosystems, especially in deeper soil profiles.

The enzyme distribution in the soil matrix reflects the dynamic interactions among the soil structure, environmental conditions, and microbial nutrient limitation (Allison et al., 2007). Microbial nutrient limitation has been studied in soil profiles (Brockett et al., 2012; Peng and Wang, 2016; Jing et al., 2017; Zuo et al., 2018). Changes in abiotic environments due to long-term climate drivers, such as alterations in soil moisture (Morugán-Coronado et al., 2019), soil pH (Rousk et al., 2010; Kivlin and Treseder, 2014), soil C:N ratio (Zhou et al., 2020) and soil type (Wakelin et al., 2008), can affect microbial nutrient limitation in complex and unpredictable ways (Burns et al., 2013; Li et al., 2018; Xu S. et al., 2020). These changes often occur in strong gradients with depth (Stone et al., 2014; Jia et al., 2019; Dove et al., 2020). Especially in agroecosystems, cropland soils have separate soil layers due to different intensities of human disturbance: topsoil (0–20 cm) and subsoil (below 20 cm; Yan et al., 2017). It is therefore not surprising that most soil properties (e.g., moisture and nutrients) and microbial communities generally vary with soil depth (Kanal and Kõlli, 1996; Li et al., 2014). More importantly, emerging evidence shows that subsoil may exhibit a stronger response to climate change in microbial activities and functioning (Fontaine et al., 2007) in association with microbial nutrient limitation. However, it remains unclear whether the relationships between microbial nutrient limitation and precipitation in topsoil and subsoil differ at the regional scale.

The framework of ecological stoichiometry provides a convenient and ready-to-use tool to better understand the ecological processes linking organisms to the environment, including linking soil enzyme activity to soil physical and chemical properties (Graham and Hofmockel, 2022). Identifying the mechanisms that govern these divergent responses of microbial nutrient limitation to precipitation in soil profiles is critical to minimize uncertainty in future soil health and function. In this study, we focused on soil enzyme activity in five soil layers of seven maize fields along a steep precipitation gradient. We examined the effect of precipitation on microbial nutrient limitation and its drivers in agroecosystem soil profiles. We developed the following hypotheses: (1) microbial nutrient limitation may exhibit more significant responses to precipitation in the subsoil than in the topsoil; and (2) the driving factors of microbial nutrient limitation change with an increase in soil depth. This study determines the microbial nutrient limitation patterns of semi-arid to humid regions and identifies drivers of variations in these patterns across soil profiles in agroecosystems.

2. Materials and methods

2.1. Study site and experiment design

The study was conducted in seven agroecosystems in the Northeast China Transect (NECT), a climatic zone with significant precipitation gradients and a critical component of the International Geosphere-Biosphere Program terrestrial transects (Zhang et al., 1997; Ni and Zhang, 2000). At latitudes ranging from 42° N to 44° N and longitudes from 123° E to 128° E within the NECT, precipitation and aridity demonstrate steep gradients (Ni and Zhang, 2000). Meteorological data that included monthly observations of the precipitation and temperature from 7 meteorological stations in Jilin Province were collected from the National Meteorological Information Center[1] for the period from 1971 to 2017. The NECT spans a wide large range of precipitation gradients from west to east, with mean annual precipitation (MAP) increasing from 300 mm to 900 mm, which MAP is the main driver of this transect. And the mean annual temperature (MAT) has slight difference among sites shown in Supplementary Table S1. We standardized our site selection by focusing on maize planting areas. These agricultural sites, which have existed for over 50 years, are located in flat areas and are managed conventionally under the same government and according to the same policies. Conventional tillage included fall plowing, spring cultivation, planting. The depth of agricultural tillage (commonly referred to as plow sole) is about 20 cm (Yan et al., 2017). Fertilizer for maize was applied with 200 kg N ha^{-1}, 70 kg P ha^{-1} and 90 kg K ha^{-1} as the base fertilizer at planting. The weeds were controlled using broad-spectrum herbicides and supplemented as required with manual hoeing (Guo et al., 2020). The soil types are classified as salt-alkali, light chernozem, chernozem, black soil, and dark brown soil, based on the Chinese soil classification system (Xiong and Li, 1987). The salt-alkali and light chernozem profile is composed of a humus layer and a compact gray-white calcium carbonate deposition layer. The organic matter content of the surface layer is 1.5 to 4.5%. There are local alkalinization and salinization, and the soil is weakly alkaline. or alkaline. The cross-section structure of chernozem has obvious humus accumulation and calcification process, the organic matter content is high (surface content is 3.5 to 12%), and the soil is neutral. The topsoil of dark brown soil and black soil is rich in humus (5 to 10%, even up to 17%), and the profile is slightly acidic (Ni et al., 1999). The basic properties of the study sites are listed in Supplementary Table S1.

2.2. Soil sampling and characterization

The seven sites, Changling (CL), Sijianfang (SJF), Nongan (NOA), Changchun (CC), Dongliao (DL), Longwan (LW) and Baihe (BH), are positioned along a precipitation gradient. Three plots (approximately 50 × 50 m) situated 50–100 m from each other were randomly selected at each site. After removing the litter and rocks, the soil was sampled by horizon to a maximum depth of 50 cm. Samples were taken discretely at five depth intervals (0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm and 40–50 cm). Three cores of soil, each with a diameter of 5.5 cm, were randomly collected and gently mixed to form one composite sample for each layer of each plot. In total, 105 soil samples (7 sites × 5 layers × 3 plots) were collected prior to maize harvest in September 2018 to minimize the effects of agricultural management. And all sampling was done within 2 days of sunny weather to ensure consistent weather and temperature.

Each sample was separated into two portions. The first fresh soil samples were immediately placed inside coolers containing ice packets for transport, returned to the laboratory, and stored at 4°C. Soil moisture (SM) was determined by oven-drying technique using 10 g of fresh soil samples dried at 105°C for 48 h to a constant weight. The amount of water in the sample can be determined and the moisture content calculated and expressed as a percentage of the dry soil weight (Schmugge et al., 1980). The second portion was air-dried for the analysis of edaphic properties. The soil pH was measured in a soil-water suspension (1:5 soil to water ratio) using a glass electrode with a pH meter (Thermo Fisher Scientific Inc., United States). Soil total carbon (TC) and total nitrogen (TN) concentrations were determined by combustion 25.000 mg of soil subsamples through a 0.149 mm mesh at 1100°C using an automatic elemental analyzer (Flash EA 1112 elemental, Italy) (Zhang et al., 2022). Total phosphorus (TP) concentration of soil was measured by first digesting 0.5 g soil sample with H_2SO_4-$HClO_4$, making up 100 ml of the digested solution, and then the TP concentration was measured using a continuous flow analyzer (SKALAR SAN++, Netherlands; Wang et al., 2022).

2.3. Soil enzyme activity

The potential activities of five hydrolytic enzymes, including two C-acquiring enzymes, β-glucosidase (BG) and β-1,4-cellobiosidase (CB), two N-acquiring enzymes, β-N-acetylglucosaminidase (NAG) and Leucine aminopeptidase (LAP), one P-acquiring enzyme, phosphatase (AP), were measured at a temperature of 25°C based on the methods described by Saiya-Cork et al. (2002) and German et al. (2011). The types, functions and substrates of soil hydrolases are detailed in Table 1. The mass of 1.5 g of fresh soil was accurately recorded and 125 ml of 50 mM acetate buffer was added. We used glacial acetic acid to adjust acetate buffer pH to the pH of this study site. The samples were homogenized by blending on highest speed for 2 min to make a slurry with a magnetic stirrer. Blank wells received 250 μl acetate buffer. Standard wells received 50 μl of standard substrate and 200 μl acetate buffer. Substrate wells received 50 μl of 200 μM enzyme substrate solution in 200 μl of acetate buffer. Sample wells received 50 μl of acetate buffer and 200 μl of soil sample suspension. Quench Control wells received 50 μl of the standard substrate (10 μM 4-methylumvelliferyl or 7-amino-4-methylcoumarin) plus 200 μl of soil sample suspension. Assay wells received 50 μl of 200 μM enzyme substrate solution and 200 μl of soil sample suspension. The pre-experimental results exhibited that the activity was the highest in the dark after 4 h of incubation at 25°C. Fluorescence plates were read at 365 nm excitation and 450 nm emission using a microplate reader (BioTek Synergy HTX, Winooski,

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[1] http://data.cma.cn/

TABLE 1 Names, Abbr. (abbreviations), functions, substrate and groups of soil enzymes that were measured in the current study.

Group	Enzyme name	Abbr.	Function	Substrate
C acquisition	β-1,4-glucosidase	BG	Cellulose degradation	4-MUB-β-D- glucosidase
	β-D-cellobiohydrolase	CBH	Cellulose degradation	4-MUB-β-D-cellobioside
N acquisition	β-1,4-N-acetylglucosaminidase	NAG	Chitin degradation	4-MUB-N-acetyl-β-D-glucosaminide
	L-leucine aminopeptidase	LAP	Peptide breakdown	L-leucine-7- amino-4-methylcoumarin
P acquisition	Phosphatase	AP	Mineralizes organic P into phosphate	4-MUB-phosphate

Vermont, United States). Eight analytical replicates were conducted per sample. Enzymatic activity was enumerated as nanomoles of substrate released per gram of dry soil and incubation time (nmol h^{-1} g^{-1}).

2.4. Quantification of microbial nutrient limitation

The soil nutrient ratios (C:N, C:P and N:P ratios) were expressed by soil elements concentration ratio. The stoichiometry of soil enzymes, such as enzyme C:N ratio, enzyme C:P ratio and enzyme N:P ratio were expressed as ln BG: ln (NAG + LAP), ln BG: ln AP and ln (NAG + LAP): ln AP, respectively. Resource limitation was measured by vector analysis of enzymatic stoichiometry (length and angle) (Moorhead et al., 2013) according to the relative activities of enzymes that acquire C, N and P. The rationale for using the relative activities of C-, N-, and P-acquiring enzymes to interpret the relative limitation of C, N, and P for microorganisms is based on ecosystem stoichiometry and metabolic theory (Allison et al., 2010). Relatively longer vector lengths express a greater C limitation, while vector angles <45° and > 45° indicate the relative degrees of N and P limitation, respectively (Moorhead et al., 2016). The vector length (unitless) and angle (°) are calculated as follows:

$$Vector\ length = SQRT\left(\left(lnBG / ln(NAG + LAP)\right)^2 + \left(lnBG / lnAP\right)^2\right)$$

$$Vector\ angle = Degrees\left(ATAN2\left(\left(lnBG / lnAP\right),\left(lnBG / ln\left(NAG + LAP\right)\right)\right)\right)$$

2.5. Statistical analysis

The Shapiro–Wilk normality test was performed using the R version 3.5.3 ‘stats’ package (R Development Core Team, 2019). We examined the relationships between precipitation and different soil properties, enzyme activities, and C:N, C:P, and N:P ratios using linear regressions. C-acquiring enzymes were calculated as BG + CB, N-acquiring enzymes were calculated as NAG + LAP, and P-acquiring enzyme was represented by AP. Redundancy analysis (RDA) was performed to analyze the relationships between soil enzyme activities and selected soil properties for 105 samples by the packages “vegan” (Oksanen et al., 2019), “adespatial” (Dray et al., 2018). We used the variation inflation factor (VIF) (“vif.cca” function) to assess multicollinearity among soil properties (VIF < 10). The significance of RDA correlations was tested Monte Carlo permutation test.

Similarly, we explored the relationships between precipitation and vector length and angle for each soil profile. The analysis of covariance (ANCOVA) was used to detect the differences in the slope of regression lines between the angle and length of vector and precipitation among soil profiles by SPSS software version 26.0 (IBM Corporation, Armonk, New York, United Stated). The angle and length of vector were dependent variables, precipitation was covariates, and soil profiles were a grouping factor with five levels. A significant soil profiles × covariate interaction would indicate that the slope of the precipitation–vector relationship differs among soil profiles. When the interaction was significant, the homogeneity of slopes assumption of ANCOVA was rejected (Poorter et al., 2008). Differences at the $p < 0.05$ level were considered statistically significant. To determine the relative influences of environmental variables on the ecoenzymatic vectors in the five soil layers, we used the rdacca.hp. function to calculate the independent adjusted R-squared (R^2) and the percentage of each explanatory variable in the RDA, running 999 permutations in the ‘rdacca.hp’ R package (Lai et al., 2022). This function performs variation partitioning and hierarchical partitioning to calculate the unique, shared, and independent contributions of each predictor to the explained variation (R^2 and adjusted R^2) in canonical analysis (RDA) by applying the hierarchy algorithm of Chevan and Sutherland (1991).

3. Results

3.1. Soil properties and nutrient stoichiometry

The physicochemical properties and soil nutrient ratios displayed various patterns in topsoil (0–20 cm) and subsoil (20–50 cm) along the precipitation gradient (Figure 1). The soil pH decreased significantly from 9.36 to 4.46 with increasing precipitation. In contrast, soil moisture and nutrients (TC, TN, and TP) were positively correlated with precipitation, but this strong correlation was not observed in the subsoil for TC. Interestingly, for these components of soil nutrient stoichiometry components (TC:TN, TC:TP, and TN:TP), significant positive relationships with precipitation were observed in the subsoil but not in the topsoil. The soil properties and the variation of soil properties with soil depth at seven sites were shown in Table 2 and Supplementary Figure S1, respectively.

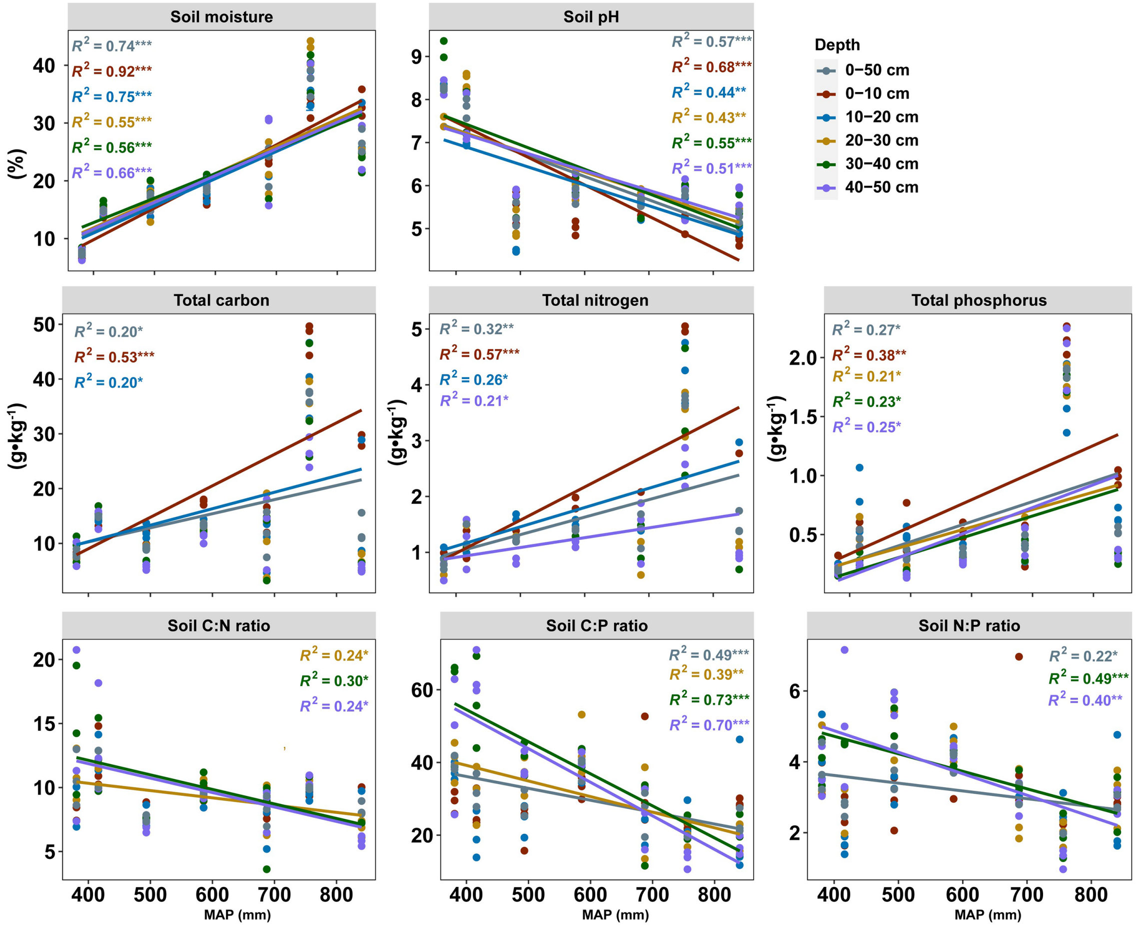

FIGURE 1
Linear regression between soil properties and MAP for each soil layer. Colored lines represent the regression of each soil layer (*n*=105). Statistics (R^2 and *p* values) for the regression are indicated using the corresponding colored text: *** p<0.001, **p<0.01, and *p<0.05. Only significant differences are shown.

TABLE 2 Soil properties and their stoichiometry from 0 to 50 cm at each sampling site.

Site	SM	pH	TC (g/kg)	TN (g/kg)	TP (g/kg)	TC:TN	TC:TP	TN:TP	Soil type
CL	0.07 ± 0.00	8.26 ± 0.04	8.20 ± 0.09	0.78 ± 0.09	0.21 ± 0.01	10.70 ± 2.19	39.74 ± 1.94	3.80 ± 0.68	Salt-alkali
SJF	0.15 ± 0.00	7.81 ± 0.23	14.88 ± 0.15	1.27 ± 0.21	0.47 ± 0.07	11.92 ± 1.66	32.12 ± 4.60	2.70 ± 0.22	Light chernozem
NOA	0.17 ± 0.02	5.30 ± 0.28	9.20 ± 0.35	1.22 ± 0.04	0.33 ± 0.04	7.53 ± 0.28	28.55 ± 3.62	3.80 ± 0.60	Chernozem
CC	0.19 ± 0.00	5.76 ± 0.18	13.39 ± 0.32	1.41 ± 0.02	0.35 ± 0.03	9.52 ± 0.17	38.51 ± 3.18	4.05 ± 0.31	Black soil
DL	0.23 ± 0.04	5.57 ± 0.08	11.68 ± 4.14	1.39 ± 0.31	0.43 ± 0.06	8.20 ± 1.19	26.36 ± 6.22	3.18 ± 0.33	Dark brown soil
LW	0.37 ± 0.02	5.73 ± 0.17	36.96 ± 1.04	3.72 ± 0.09	1.88 ± 0.04	9.94 ± 0.10	19.69 ± 0.12	1.98 ± 0.01	Dark brown soil
BH	0.27 ± 0.02	5.27 ± 0.13	12.56 ± 2.62	1.50 ± 0.21	0.53 ± 0.03	8.31 ± 0.55	23.52 ± 3.44	2.82 ± 0.22	Dark brown soil

Values were presented as means ± SD. SM, soil moisture; pH, soil acidity and alkalinity; TC, total carbon; TN, total nitrogen; TP, total phosphorus. TC:TN, TC:TP and TN:TP were calculated to represent soil total C:N, C:P and N:P concentration ratios.

3.2. Soil enzyme activity and stoichiometry across precipitation gradient

The soil enzyme patterns were dissimilar to soil nutrient patterns along the precipitation gradient (Figure 2). C-acquiring enzyme activities were unaffected by precipitation. The N-acquiring enzyme activities decreased across the precipitation gradient in all soil profiles, while P-acquiring enzyme activities were positively correlated with precipitation at a depth of 0–30 cm but not at that of 30–50 cm. The C:P enzyme stoichiometry pattern was the opposite of that of the P-acquiring enzyme. With increasing precipitation, the enzymatic C:N and N:P ratios demonstrated increasing and decreasing trends, respectively; however, both stoichiometries responded to precipitation more drastically in the subsoil than in the topsoil. The variation of soil enzyme activities and stoichiometry with soil depth at seven sites was shown in Supplementary Figure S2. The major environmental variables shaping the soil enzyme pattern were determined through RDA (Figure 3). According to the RDA results, approximately 33.58% of the variance in total soil enzyme activity can be explained by environmental variables. The first two RDA axes explained 30.04% of the relationships between enzymes and the environment (24.79 and 5.25% for the first and second axes, respectively). According to the model selection results, soil pH and moisture were the most important factors affecting the enzyme activity.

3.3. Soil microbe metabolic limitation and its driving factors

The nutrient limitation of soil microbes was calculated using enzyme stoichiometry and quantified by vector angle and length (Figure 4). Vector angles ranging from 36.1° to 80.5° were positively related to the precipitation, and they displayed a more intense correlation with precipitation in the subsoil than in the topsoil (Figure 4A; Supplementary Table S2). We also subdivided the driving factors for nutrient limitation according to the soil layer (Figure 5). We observed that pH had the largest independent effects on vector angle in topsoil, explaining 69.41 and 44.78% of the variance in the depth ranges of 0–10 cm and 10–20 cm, respectively (Figure 5A). From the topsoil to the subsoil, the soil physicochemical properties (soil pH and moisture) variance explanation ranged from 85.64 to 16.79% (Figure 5A). In contrast, the interpretations of soil nutrients and their stoichiometry ranged from 14.36 to 83.21% (Figure 5A). Vector length was positively correlated with precipitation only in the subsoil (Figure 4B). The interpretation of soil nutrient stoichiometry with respect to the vector length grew stronger with depth (Figure 5B). Furthermore, it was not found that the temperature would have an effect on our results by redundancy analysis and hierarchical partitioning analysis.

4. Discussion

4.1. Spatial variations of soil properties along the precipitation gradient

Soil moisture, total carbon, total nitrogen, total phosphorus increased as the MAP increased along the NECT, but the soil pH decreased as the MAP increased. These results are consistent with the results at the regional scale (Wang et al., 2002; Cui et al., 2019a). Due to the steep moisture gradient, the virgin vegetation changes gradually from mixed deciduous broad-leaved forest to meadow steppe along the transect (Prentice et al., 2011). The forest can improve the availability of soil nutrients by nitrogen fixation and phosphorus strategies (Nasto et al., 2014, 2017). In addition, soil properties are related to the interaction of precipitation and soil parent materials (Huston, 2012). The high pH of the soil in west of the transect is due to the fact that the soil is salt-alkali and the evaporation is three to four times higher than the precipitation (Wang and Ba, 2008; Yang et al., 2021). Therefore, less precipitation, high surface evaporation and parent salinity are the major reasons for high soil pH. Understanding soil properties at the regional scale is fundamental to predicting climate changes at the global scale.

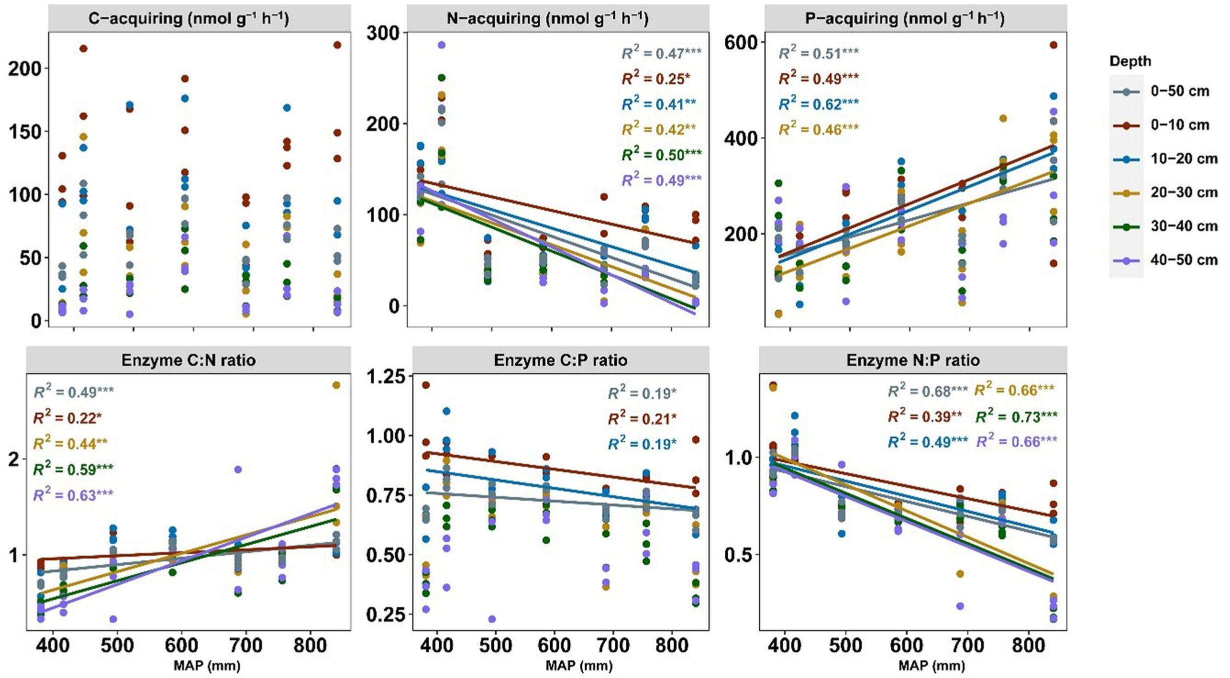

FIGURE 2
Patterns of enzyme activity and stoichiometry along the precipitation gradient for each soil layer. Colored lines represent the regression of each soil layer (*n*=105). Statistics (R^2 and *p* values) for the regression are indicated using the corresponding colored text: *** $p<0.001$, ** $p<0.01$, and * $p<0.05$. Only significant differences are shown. C, N, and P represent carbon, nitrogen, and phosphorus.

4.2. Patterns of microbial nutrient limitation across precipitation regions throughout soil profiles

We did not observe a significant relationship between C-acquiring enzymes and precipitation (Figure 2), and surprisingly, the vector length increased with precipitation, indicating that microbial C limitation was gradually exacerbated along the precipitation gradient in 0–50 cm. Moreover, N-acquiring enzyme activity decreased and P-acquiring enzyme activity increased with increasing precipitation (Figure 2), which alters the stoichiometry of enzymes leading to C limitation. We attributed this pattern of microbial C limitation to changes in soil nutrients and their stoichiometry across precipitation regions (Figure 5B). Microbial resource limitation is relative (Chen et al., 2018); thus, microbial C limitation can depend on the combined effect of other nutrients.

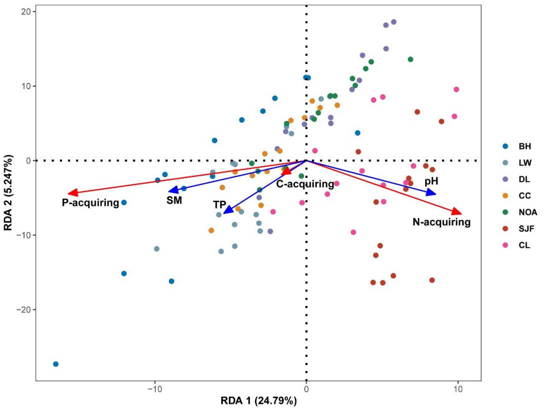

FIGURE 3
Redundancy analysis of 105 soil samples based on soil enzyme activity and dominant environmental factor ordination biplot. The overall model is significant (p<0.001). Environmental factors: SM, soil moisture; pH, soil acidity and alkalinity; TP, total phosphorus. Site: BH, Baihe; LW, Longwan; DL, Dongliao; CC, Changchun; NOA, Nongan; SJF, Sijianfang; CL, Changling.

We detected a decrease in the enzymatic C:P and N:P acquisition ratios with increasing precipitation (Figure 2). Microorganisms can shift from secreting more C-acquiring enzymes and N-acquiring enzymes to secreting more P-acquiring enzymes, which implies an increased demand for P. Moreover, the vector angle became greater than 45° with increasing precipitation (Figure 4A). Our results notably indicated that microbial P limitation was gradually exacerbated along the precipitation gradient. A perpendicular projection of P-acquiring enzyme onto the line overlaying the environmental variable arrow revealed that P-acquiring enzyme was influenced by soil pH and moisture (Figure 3). P is predominately derived from mineral aerosol deposition and weathering, and it is highly dependent on pH (Thingstad et al., 2005; Mahowald et al., 2008). High soil moisture and low soil pH increase P-acquiring enzyme activity, which facilitates P solubilization (Collavino et al., 2010; Xu Z. et al., 2020). In addition, soil pH and moisture were the main factor determining the pattern of soil enzymes along the precipitation gradient (Figure 3). Therefore, soil pH and moisture play an essential role in microbial P limitation throughout soil profiles.

Furthermore, soil nutrients and their stoichiometry and soil physicochemical properties are equally important for microbial phosphorus limitation in 0–50 cm (Figure 5A). More C and N might lead to microbial P limitation (Cui et al., 2020). This observation may be explained for two reasons. On the one hand, if the C and N accumulated in the soil reduces the relative concentration of soil P, the microorganisms may be limited by P due to the elemental stoichiometric balance of the microorganisms (Sinsabaugh et al., 2008, 2009; Chen et al., 2017). Thus, despite the increase in soil P, microbial P limitation remains because of the slow growth rate of P relative to that of C and N. On the other hand, phosphatases have relatively high C and N concentrations, and microorganisms require sufficient C and N to construct extracellular phosphatases (Treseder and Vitousek, 2001; Houlton et al., 2008). Phosphatase may be highly responsive to changes in soil elements, a critical strategy for organism adaption to

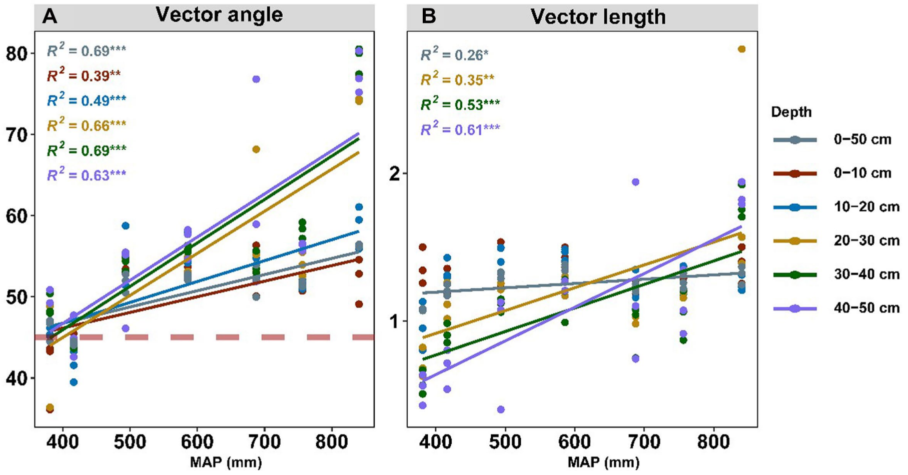

FIGURE 4
Effects of MAP (mm) on microbial N/P limitation **(A)** and microbial C limitation **(B)**. Soil microbial N/P limitation is represented by vector angles: >45° represents P limitation, and <45° represents N limitation. Soil microbial C limitation is represented by vector lengths, where microbial C limitation increases as the values increase. MAP represents mean annual precipitation.

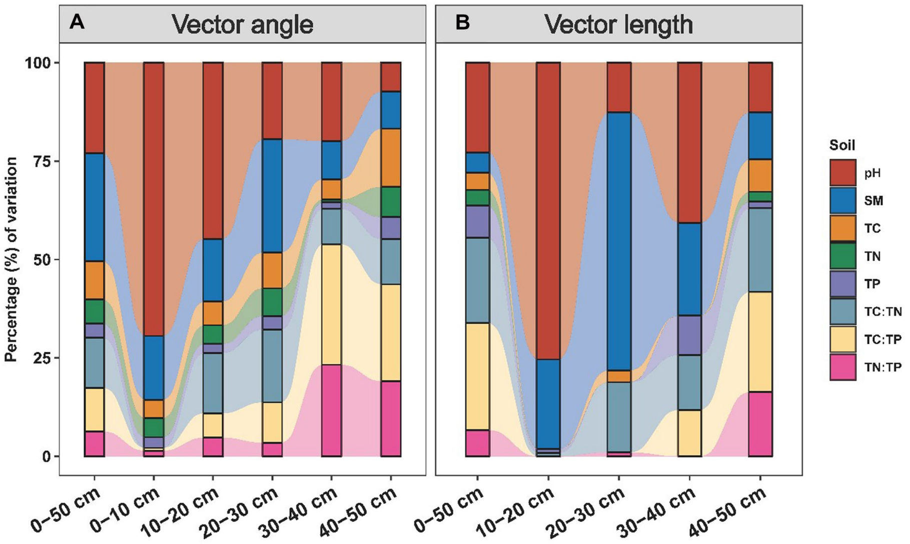

FIGURE 5
Influences of soil variables on vector angles **(A)** and lengths **(B)**. Percentage of variation in vector angles and lengths explained by soil variables. SM, soil moisture; pH, soil acidity and alkalinity; TC, total carbon; TN, total nitrogen; TP, total phosphorus.

human modifications of the global biogeochemical cycle that can delay the onset of P limitation (Güsewell and Freeman, 2005; Marklein and Houlton, 2012). These findings demonstrate that precipitation regulates soil physicochemical properties and nutrient status (Smith, 2011; Ma et al., 2015), which consequently greatly enhances microbial C and P limitation. Our current results take a new step and are valuable for understanding microbial nutrient limitation along the precipitation gradient in agroecosystems.

4.3. Contrasting mechanisms governing microbial nutrient limitation in topsoil and subsoil

Our findings are in support of our hypothesis that microbial nutrient limitations were stronger in the subsoil than in the topsoil along the precipitation gradient. Also, we show that the driving factors of microbial nutrient limitation are different in topsoil and subsoil. Soil properties and enzyme activities can change with soil profiles (Stone et al., 2014; Li et al., 2020; Luan et al., 2020), and we observed wide differences in soil and enzyme stoichiometry between the topsoil (0–20 cm) and subsoil (20–50 cm). Our study found that enzymatic C:P acquisition ratios were negatively correlated with precipitation only in the topsoil, which is attributable to the phosphatase distribution pattern. Enzymatic N:P acquisition ratios decreased, but enzymatic C:N acquisition ratio increased along the precipitation gradient, and changes substantially in the subsoil. The vector angles visualized that microbial P limitation increased and responded more strongly to precipitation in the subsoil than in the topsoil. In topsoil, soil pH and moisture are the major drivers of microbial P limitation (Figure 5A). Soil pH governs phosphatase spatial variations and is positively correlated with enzymatic C:P and N:P acquisition ratios (Xu et al., 2017). It is interesting to note that, compared to the topsoil, soil nutrient availability and their stoichiometry are important factors in determining microbial P limitation in subsoil (Figure 5A). Soil substrate availability greatly influences enzyme activity patterns (Stock et al., 2019), and low resources (C and N) and O_2 concentrations can limit microbial metabolism (Fierer, 2017; Gu et al., 2017). Zhou et al. (2020) also found that the soil C:N ratio explains a large proportion of the variation in microbial nutrient acquisition. Emerging evidence suggests that subsoils, exhibit more varied organic matter sources, microbial communities, and substrate availability compared to those of the topsoil (Rumpel et al., 2012; Chen et al., 2019). Differences in soil properties across soil depths can lead to greater environmental filtering or competition for nutrients among microorganisms than in the topsoil (Bahram et al., 2015; Schlatter et al., 2020). Especially in agroecosystems, this difference between topsoil and subsoil may be attributed to the agricultural tillage depth, which is typically 0–20 cm. Cropland activities contribute to the homogenization of microbial communities (Rodrigues et al., 2013), and alter microbial resource limitations (Cui et al., 2021). On the contrary, the original soil conditions were preserved in the subsoil, resulting in microbes secreting soil enzymes that are less responsive to precipitation in the topsoil than that in the subsoil and attenuate the reaction of microbe nutrients limitation to precipitation in the topsoil.

Ecosystems cannot be limited by carbon or nutrients alone (Soong et al., 2020), and most microbial communities are co-limited by energy and key nutrients (Moorhead et al., 2016). Another marked trend is that the vector length increases in the subsoil with precipitation. This result indicates that microbial C limitation increased in the subsoil along the precipitation gradient. The detected relationships might result from that soil C:N and C:P ratios progressively decline across the precipitation region in the subsoil (Figure 1), which can lead to insufficient soil C (Chen et al., 2018). In contrast, there is no relationship between microbial C limitation and precipitation in topsoil. This might occur because the effect of precipitation is masked by cropland activity, causing soil nutrient stoichiometry in topsoil that exhibited no response to precipitation.

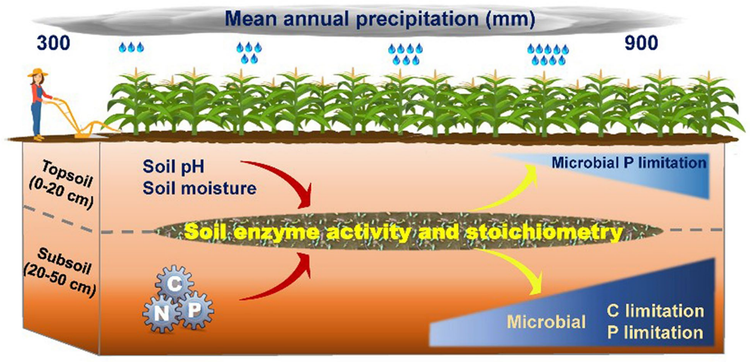

FIGURE 6
A conceptual framework of soil enzyme activity and stoichiometry along a precipitation gradient (300–900 mm) among soil profiles in agricultural ecosystems. Microbial C limitation, microbial carbon limitation; Microbial P limitation, microbial phosphorus limitation. pH, soil acidity and alkalinity; C, total carbon; N, total nitrogen; P, total phosphorus.

Moreover, soil nutrients and their stoichiometry increase in their interpretation of C limitation with depth (Figure 4). Therefore, soil C:N:P stoichiometry tremendously affected microbial groups involved in major biogeochemical processes (Luo et al., 2020). Additionally, balanced nutrient stoichiometry is essential for maintaining microbial and elemental homeostasis (Cui et al., 2019b).

Further, P limitation changes rapidly in the subsoil, which contributes to C limitation. Nutrients are interdependent and they have a complex coupling, so changing in one nutrient cycle type can alter the availability of another nutrient (Marklein and Houlton, 2012). The role of P limitation in the storage capacity of the C ecosystem has previously been substantially underestimated (Peng and Thomas, 2010). P affects the C-storage capacity both directly and indirectly by affecting the plant growth capacity and limiting biological activities for N fixation (Peñuelas et al., 2012). A model predicted less efficient microbial growth in P-limited soils, indicating that P availability may affect C cycling (Waring et al., 2014). These nutrient interdependencies confirm that resource limitation coupling is complex, and excess precipitation leads to depletion of P and C and induces imbalances in agroecosystems. Our results highlight the contrasting mechanisms governing microbial nutrient limitation in topsoil and subsoil. Microbial P limitation was controlled by the soil pH and moisture in the topsoil, while microbial C and P limitation in the subsoil were regulated by the soil nutrients and their stoichiometry (Figure 6). The findings suggest that ecosystem functions and microbial nutrient limitation cannot be comprehensively assessed from topsoil observations alone.

Ecological stoichiometry is commonly applied to explore relationships between brown food webs such as soils and microbes (Bell et al., 2014). When nutrient-limited, microorganisms reduce their uptake of C for nutrients and excrete excess C through enzymes and respiration, so that the ability to assimilate C into biomass tends to decrease (Manzoni et al., 2017). Nutrient-deprived foods are stoichiometrically unbalanced, due to differences in elemental concentrations in food and consumers reflecting stoichiometric mismatches that limit consumer growth and development, thereby affecting the metabolism and function of the brown food web (Filipiak, 2016). Further studies on soil profiles, we found that global change-induced stoichiometric mismatch in agricultural subsoil is more severe. Our results are an important step forward in better understanding soil microbial metabolism across the whole profile of agroecosystems under changing precipitation patterns. Future research could aim to study the metabolic capacity of brown food webs under precipitation changes through metagenomic next-generation sequencing to better understand how precipitation affects the function of whole-profile brown food webs in agroecosystems.

5. Conclusion

We observed an increase in microbial C and P limitation along the precipitation gradient in agroecosystems. Furthermore, our study showed stronger microbial P limitation in the subsoil compared to the topsoil. Given that the high sensitivity of microbial nutrient limitation was observed in the subsoil, our results suggest that the impact of precipitation on microorganisms may be underestimated if only the topsoil is assessed, especially in agroecosystems. Our study also provides insights to elucidate the differentiation in microbial nutrient limitation mechanisms among soil profiles, generating realistic predictions of how agroecosystems will respond to ongoing climate changes. Future research will incorporate deep tillage to maintain microbial nutrient balance in the subsoil to meet production goals and protect vital life-support systems in the context of climate change.

Data availability statement

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

Author contributions

JY: conceptualization, methodology, software, formal analysis, investigation, and writing—original draft. PG: methodology, formal analysis, data curation, and writing—review and editing. PZ:

validation, investigation, and resources. YW: investigation, resources, visualization, and writing—review and editing. DeW: conceptualization, supervision, writing—review and editing. DoW: conceptualization, supervision, resources, writing—review and editing, project administration, and funding acquisition.

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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.2023.1137172/full#supplementary-material

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Optimizing the distribution pattern of species under climate change: the protection and management of *Phellodendron amurense* in China

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Objective: *Phellodendron amurense*, a special species in Northeast Asia, is the source of the wild medicinal Phellodendri Amurensis Cortex, the second-level key protection in China. Because of its dual value of medicine and timber, it has been cut in large quantities, resulting in a sharp decline in wild resources. It has been listed as a national first-class rare tree species. Here, we aim to plan protection area and wild tending area for Chinese *P. amurense* in the context of climate change.

Method: In this study, based on the Biomod2 model, the main environmental factors affecting the distribution and the potentially suitable areas of the current and future were investigated. Furthermore, the correlation between the main environmental factors and the chemical components was determined by full subset regression. Habitat quality and landscape pattern change were determined by InVEST and Fragstats software based on the land use data in 1980, 2000, and 2020. Then, Zonation software was used to plan the priority protection and wild tending areas.

Results: The results showed that in the future, the potential habitat of *P. amurense* will gradually move to the high latitude and high altitude areas in the northwest direction, and the high suitability area will decrease sharply. Since 1980, the habitat quality of *P. amurense* habitat has gradually deteriorated, and the fragmentation has gradually intensified. In the future, the central part of the Greater Khingan Mountains and the forest area of the Lesser Khingan Mountains will be the long-term stable sanctuary. Fengcheng City and Tonghua County are the most suitable for the wild tending areas.

Conclusion: The existing nature reserve only contains 6.01% of the priority protection area, so we propose to expand the area to cover a larger proportion of the sanctuary and implement management and restoration plans to increase the suitability and connectivity. These results can support the protection action and provide a reference and scientific basis for further research, rational development, and utilization of *P. amurense*.

KEYWORDS

***Phellodendron amurense*, climate change, ecological niche modeling, landscape pattern, habitat quality, conservation management**

1. Introduction

In large-scale space, climate plays an important role in determining the spatial and temporal distribution of species, and the reason why species can only grow in an environment is that species adapt to specific climatic conditions within their geographical range (Araújo et al., 2005; Pant et al., 2021). Since the 19th century, due to the intensification of human activities, the global temperature has increased by around 1°C on average (Sommer et al., 2010; Ma et al., 2022). In response to climate change, the geographical distribution of many plants will change (Zhao et al., 2021). Compared with the past migration rate of plant species, many plants may not be able to adapt to the current rapid climate change (Huntley, 1991; Davis and Shaw, 2001; Elias et al., 2017). The average lifespan of individuals and the age at the time of reproductive maturity partly determines the adaptation potential of plant populations to climate change. Subject to other conditions, due to the length of generation and lifespan, annual plants adapt faster to climate change, while perennials adapt more slowly (Jump and Peñuelas, 2005). Rapid climate change may pose a more serious threat to some endangered woody plants' survival.

Phellodendron amurense, a deciduous tree of the genus *Phellodendron* of Rutaceae (**Figures 1B–D**). It is an endemic species in Northeast Asia (Ma et al., 2015). And it is mainly distributed in China, the Far East of Russia, the Korean Peninsula, and Japan (Wei et al., 2019). In China, *P. amurense* is mainly distributed in the Northeast China and North China (Chinese Botanical Society, 1997), which is a national first-class rare tree species, second-class protected plant, and second-class key protected wild medicinal material in China. Its bark is called "Phellodendri Amurensis Cortex," a rare traditional Chinese medicine with anticancer and antiviral effects (Zhao et al., 2013; Zhang and Zhang, 2019; National Pharmacopoeia Commission, 2020). It is also one of the three famous hardwoods in Northeast China, which has important ecological and economic value (Zhang and Wang, 2014). Since the 1980s, wild resources have been plundered and seriously damaged due to their high commercial value. In addition, the poor self-renewal ability has further exacerbated the sharp decline of wild resources (Zhang et al., 2016), leading to a serious imbalance in the supply relationship.

The conservation of rare species has shifted from focusing on the intrinsic value of species to conservation ecosystem services and the benefits provided to people (Groner et al., 2023). The establishment of nature reserves is the most effective means to slow down the rate of species extinction. However, the current nature reserves are mostly designed according to the current distribution of species, which is difficult to meet the needs for habitat protection under future climate change (Ran et al., 2019). In addition, wild tending is also another way to protect wild resources, which represents a way of artificially or naturally increasing the population size in its native or similar environment based on the growth characteristics of the target species and their requirements for ecological environment conditions, so that its resources can be collected and utilized by people and can continue to maintain community balance (Chen et al., 2004). This approach can not only solve the shortage of medical resources but also promote the recovery of the population (Chen et al., 2016). The production and change of effective components of medicinal plants have a strong correlation and correspondence with the environment (Zeng et al., 2015). Therefore, the relationship between the quality of medicinal plants and their habitat must be considered before specifying the wild tending plan (Shen et al., 2021).

This study constructed a new analytical framework. In this framework, ten species distribution models based on the Biomod2 were used to identify the main environmental factors affecting the spatial distribution of *P. amurense* in the Chinese region, and the correlation between the main environmental factors and chemical components content was clarified using full subset regression. Then, we combined the above analysis results with land use data to evaluate the changes in the landscape pattern of the habitat of *P. amurense*, and planned priority protected areas and wild tending areas. In addition, the framework takes into account the synergistic effect of habitat fragmentation and climate change, and aims to provide support for the conservation action and sustainable use of resources of *P. amurense* in China under the background of global climate change. Meanwhile, this framework can also provide effective reference for the management of medicinal plant resources in China. The purpose of this study is to: (1) determine the environmental factors that limit the distribution of *P. amurense* and their correlation with the chemical components in China; (2) explore the influence of climate change on the distribution of *P. amurense* in China; (3) explore the habitat quality and connectivity of the habitat of *P. amurense* in China; (4) plan the priority protection and wild tending areas of *P. amurense*, and propose protection management strategies in China; (5) provide a reference method for the protection of other rare and endangered wild species.

2. Materials and methods

2.1. Occurring data source and processing

This study obtains the distribution data of *P. amurense* in three ways: (1) Field investigation. From July to September 2017–2022, an extensive survey was conducted, totaling 185 geographical points; (2) Network database. The Global Biodiversity Information Facility,[1] the Chinese Virtual Herbarium,[2] and the National Specimen Information Infrastructure [3]have collected 154 geographical occurrence points of *P. amurense* from 2000 to now; (3) Literature search. A total of 118 geographical data points have been collected through Google Academic, CNKI, and other platforms (e.g., Wan et al., 2014; Zhang et al., 2016). Google earth pro software (Google Earth USA) was used to eliminate the unreasonable geographical location data of *P. amurense* in waters and cultivated land. The "spThin" package in R 4.1.0 eliminates the geographic location data gathered within 10 km (Aiello-Lammens et al., 2015). Finally, we reserved 193 geographical data points of *P. amurense* for modeling (**Figure 1A**).

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[1] https://www.gbif.org

[2] http://www.cvh.ac.cn

[3] http://www.nsii.org.cn

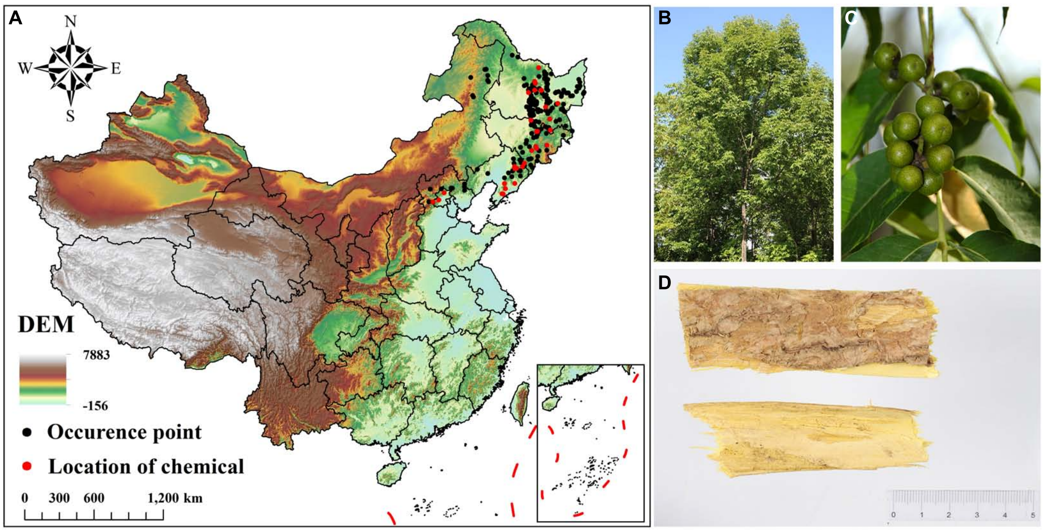

FIGURE 1
Occurrence data and morphological characteristics of *Phellodendron amurense*. **(A)** Occurrence data and geographical distribution of chemical components of *P. amurense*; **(B)** Plants of *P. amurense*; **(C)** Fruits of *P. amurense*; **(D)** Bark of *P. amurense* (medicinal material).

2.2. Source and processing of environmental factor data

Phellodendron amurense is a sun loving plant, and solar radiation plays an important role in its growth, and its suitability for soil is extremely strong (Tang et al., 2014). Therefore, 31 environmental factors were selected for this study, including solar radiation and biological climate factors (**Supplementary Table 1**). Srad01-12 were downloaded from the WorldClim Database (v2.1),[4] covering 1970–2000. In order to make environmental data more representative of current climate conditions as much as possible, we downloaded monthly mean minimum temperature, monthly mean maximum temperature, and monthly mean precipitation data (2000–2018) from the WorldClim Database (v2.1). Then, we used the biovar package in R 4.1.0 to calculate 19 climate factors (2000–2018). This study used the MaxEnt3.4.4 software to establish an initial model (modeling ten times) without adjusting parameters. Environmental factors with relative contribution rates of less than 1% were removed. Moreover, the correlation function in ENMTools software was used to conduct correlation analysis on the remaining environmental factors (Warren et al., 2010). Then, we screened the two environmental factors with $|r| > 0.80$ and retained the environmental factors with a larger contribution rate to prevent the high correlation between environmental factors from causing an over-fitting species distribution model (Goldsmit et al., 2020; Gomes et al., 2020). Finally, eight environmental factors were retained for final modeling.

We selected CNRM-CM6-1, MIROC-ES2L, and MRI-ESM2-0 general atmospheric circulation models from the WorldClim Database (v2.1) to establish the future species distribution model. Each model includes 4 years: 2021–2040 (2030s), 2041–2060 (2050s), 2061–2080 (2070s), and 2081–2100 (2090s). Each year includes four shared socio-economic paths (SSPs): SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. The four selected carbon emission scenarios, SSP1-2.6 to SSP5-8.5, represent the radiative forcing scenario from low to high (Jiang et al., 2020). In order to avoid the uncertainty caused by the prediction of a single general atmospheric circulation model (GCM), we used ArcMap10.5 software to average the data of three climate models in the same year and the carbon emission scenario. Because there is no matching future data for solar radiation data, in this study, we used solar radiation as a static variable in the species distribution modeling. The spatial resolution of the above environmental data is 2.5 min.

In this study, land use change in the suitable areas of *P. amurense* was compared using 1980, 2000, and 2020 land use data from the Resource and Environment Science and Data Center[5] with a spatial resolution of 1 km. We reclassified them into cultivated land, forest, grassland, waters, construction land, and unused land.

2.3. Construction of species distribution model

The "Biomod2" package in R 4.1.0 integrates ten common species distribution models (GLM, GBM, GAM, CTA, ANN, SRE, FD, MARS, RF, and MaxEnt). This study used this package to simulate the spatial distribution of *P. amurense* and analyzed the relative importance of environmental factors used in modeling (Elias et al., 2017; Xu et al., 2021). Except for the MaxEnt model, all models were built with default parameters. The "kuenm" package in R 3.6.3 was used to evaluate the performance of the MaxEnt model under different combinations of multiplicators (RM) and eigenvalues (FC). A total of 572 candidate models

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[4] www.worldclim.org

[5] https://www.resdc.cn/

were constructed by combining 17 regularization multiplier values (0.10–1, interval 0.10; 2–6, interval 1; 8, 10) and five features provided by the MaxEnt model (linear feature: L, secondary feature: Q, fragmentation feature: H, product feature: P and threshold feature: T). The optimal model is selected according to the delta in the Akaike information criterion (AICc) model. When the AICc value is minimum (deltaAICc = 0), it is considered the optimal model (Cobos et al., 2019). The optimized MaxEnt3.4.4 software parameters are RM = 0.30 and FC = LQP.

In Biomod2 package, 75% of the distribution data was set as training data and the other as testing data. The division of training data and testing data was repeated five times. In order to better simulate the actual distribution and reduce the spatial deviation, 5,000 pseudoabsence points (repeated three times) were randomly created to construct the model. In the end, 150 model results were constructed in this study. The most accurate way to verify the prediction accuracy of SDMs is to combine the true skill statistic (TSS) and the area under the receiver operating characteristic curve (AUC) to evaluate the model results (Bucklin et al., 2015; Zhang et al., 2020). The TSS value ranges from −1 to 1, and the AUC value ranges from 0.5 to 1. The closer the value is to 1, the stronger the model's prediction ability is (Freitas et al., 2019; Zhao et al., 2021). For 150 model calculation results, models with an average TSS greater than 0.80 and an average AUC greater than 0.90 were used to calculate the final species distribution layer.

2.4. Classification of suitable areas and analysis of climate characteristics

We used the maximum training sensitivity plus specificity threshold (in this study is 0.375), which can maximize the TSS value to create a binary mapping, and has been proven to produce the most accurate prediction (Jiménez-Valverde and Lobo, 2007; de Andrade et al., 2020). Three grades of the suitable area were divided: low suitability area (0.375–0.50), medium suitability area (0.50–0.70), and high suitability area ($\geq$0.70) (Chen et al., 2022). In order to compare the changing trend of the spatial pattern of *P. amurense* suitable area under the current and future climate, the Distribution Changes Between Binary SDMs tool in SDMTools (ArcMap10.5) was used to calculate the area of expansion, stability, and contraction. The centroid changes (lines) tool was used to calculate the centroid migration trend (Brown, 2014).

In order to analyze the changes in environmental characteristics in the current potential area, we randomly selected 1,000 points in the current distribution area. Then, we extracted the corresponding values of the 1,000 distribution points in the different climate conditions layer corresponding to the leading environmental variables. The average value and 95% quantile of the extracted value were calculated, and the density map was drawn to intuitively understand the environmental pressure that *P. amurense* will face in the future (Tagliari et al., 2021).

2.5. Habitat quality assessment of habitat

In order to find out the current and past changes in the habitat quality of *P. amurense* habitat, the Habitat Quality Model in the InVEST model was used to quantify the habitat quality in the study area (Akbari et al., 2021). The value of the habitat quality index is between 0 and 1. The higher the value, the better the habitat quality in the region (Liu et al., 2021). Because of the distribution characteristics of the *P. amurense* natural population, only forest landscape was used as the evaluation object. Cultivated land, urban land, rural residential land, and construction land were considered as threat sources of the habitat. The impact weights and distances of these four threat sources were assigned (**Supplementary Table 2**), and the habitat suitability of different land uses and their sensitivity to threat sources were determined (**Supplementary Table 3**; Yang et al., 2018). Finally, the results were classified by the natural discontinuities method. By doing this, we obtained low, medium, and high-quality habitats of *P. amurense*.

2.6. Habitat landscape pattern analysis

The landscape index was used to quantitatively study the degree and process of fragmentation in the suitable area of *P. amurense* based on the land use data in 1980, 2000, and 2020. Seven landscape indexes were calculated, including the number of patches (NP), the patch density (PD), the mean patch size (AREA_MN), the area-weighted mean shape index (SHAPE_AM), the area-weighted mean patch fractal dimension (FRAC_AM), the division index (DIVISION), and the aggregation index (AI). The spatial distribution pattern of seven landscape indexes in three periods was calculated using the moving window method of FRAGSTATS 4.2 software. Moreover, the specific method is shown in the literature (Ran et al., 2019). According to the growth environment of *P. amurense*, the forest land use type was selected to represent the landscape fragmentation degree of the natural population.

ArcMap10.5 was used to carry out dimensionless standard normalization processing for each index, and then principal component analysis (PCA) and calculation were carried out for the seven indexes in each period. The principal component whose cumulative contribution rate was greater than 98% was selected. The weighted sum tool in ArcMap10.5 was used to perform overlay analysis on the layers with the weight of each principal component as the coefficient. Finally, the habitat fragmentation layers of *P. amurense* in different periods were obtained through range standardization (**Supplementary Table 4**; Ran et al., 2019).

2.7. Prediction of chemical composition and correlation with environmental factors

In this study, a parameter relationship model was established between the chemical composition content of Phellodendri Amurensis Cortex and environmental factors to obtain high-quality medicinal materials range of wild tending areas. In order to ensure the consistency of data, we screened the collected data and literature, used the content of 31 groups of Berberine and Palmatine in the same literature, and obtained the relevant geographical location information (**Figure 1A**; Zhang, 2015). These geographical location data were also used to model the species distribution of *P. amurense*.

Based on the MuMIn (Multi-Model Interference) package in R 4.2.1, the correlation between chemical component content and environmental factors was analyzed by full subset regression (Xu et al., 2020). The method of full subset regression is to fit all the combination models that may appear in the prediction variables in this model in turn and screen the best model under the conditions of existing variables according to a certain standard (such as R^2, AIC, and SBIC) (Ren, 2022). Selected the best model by adjusting AIC and used p-value to indicate the correlation between environmental factors and the chemical content of Berberine and Palmatine. A value less than 0.10% indicates a very significant correlation, a value range of 0.10–0.50% indicates a significant correlation, and a value range of 0.50–1.00% indicates a correlation. The specific formula is as follows:

$$C = \beta_1 x_1 + \beta_2 x_2 + +\beta_i x_n$$

Where C is the content of chemical components, x_n is the environmental variable, and β_i is the regression coefficient, the results were evaluated using the coefficient of determination (R^2) and F-test (Eberly, 2007).

In order to quantify the distribution of each chemical component in space, the "raster calculator" function in ArcMap10.5 was used. According to the coefficient of each environmental factor in the regression equation, the environmental factor layer of Berberine and Palmatine in the suitable area of *P. amurense* was standardized after the Z-Score superposition. By doing this, we obtained the chemical composition distribution layer of Berberine and Palmatine.

2.8. Planning of priority protection areas and wild tending areas

In order to serve the protection action of *P. amurense* under the background of climate change, the core area partitioning algorithm in Zonation 4.0 software[6] was used in this study. We input layers of the current and future suitable areas, habitat quality, and landscape fragmentation in the model to plan the priority protection area. The weights of all the layers were set as 1, and other parameters were the default values of the model. We set the warping factor to "1" and removed one grid at a time to optimize the results (Moilanen, 2007). Then, we classified the output results: the top 5% were taken as the high protection areas, 5–10% as the moderate protection areas, and 10–20% as the low protection areas (Moilanen et al., 2005).

Considering that development and constructive activities are forbidden in nature reserves, the existing protection areas and planned protection areas in China were removed from the current high suitability of *P. amurense*. Then the spatial distribution layer of Berberine and Palmatine content and the remaining areas of the current high suitability were input in Zonation software. The parameters were the same as planning the priority protection area. The natural discontinuity method is based on the natural grouping inherent in the data, identifying the classification interval, which can most appropriately group similar values, and maximize the differences between various classes (Li and Xu, 2020). Therefore, the low, medium, and high-quality wild tending areas of *P. amurense* were obtained by classifying the result by the natural discontinuity method.

3. Results

3.1. Distribution of current potential distribution and landscape pattern change of *P. amurense*

Under the current climate conditions, the suitable habitat of *P. amurense* is mainly distributed in Changbai Mountain, Longgang Mountain, Zhangguangcai Mountain, and Lesser Khingan Mountains, which formed an inverted triangle. And there are also a few parts in the Yanshan Mountain and the south-central part of the Greater Khingan Mountains (**Figure 2a**). The total area of suitable habitat is about 55.63 × 10^4km^2. Specifically, the high suitability area is about 29.95 × 10^4km^2. This area is mainly distributed in the southeast of Changbai Mountain, Zhangguangcai Mountain, Longgang Mountain, and Lesser Khingan Mountains, and a small amount in the middle of the Greater Khingan Mountains, the northern branch of Changbai Mountain and the middle of Yanshan Mountain. The medium suitability area is about 15.79 × 10^4km^2. This area is mainly distributed in the surrounding area of high suitability and with a scattered dotted distribution in the Yanshan Mountains. Moreover, the low suitability area is about 9.59 × 10^4km^2, mainly distributed in the marginal area connecting the medium suitability and non-suitability areas (**Figure 2a**).

At present, there are six types of land use in the suitable habitat, including forest, grassland, waters, cultivated land, construction land, and unused land, of which the forest area is the largest, about 30.46 × 10^4km^2, accounting for 31.85% of the total suitable area (**Figure 2b**). We used land use data to analyze the forest landscape pattern and fragmentation in the suitable habitat. A high fragmentation is found mostly at the edge of the landscape (**Figure 2c**). Furthermore, seven landscape pattern indexes increased or decreased year by year, showing a trend of gradual fragmentation. From 1980 to 2020, NP and PD increased by 6.36 and 5.97%; AREA_AM decreased 9.49% compared with 1980; SHAPE_AM decreased from 44.636 to 40.467; FRAC_AM decreased from 1.280 to 1.275; DIVISION increased by 0.022, 2.48% higher than that in 1980; and AI decreased by 0.648, or 0.79% (**Figure 2d**).

3.2. Habitat quality change of *P. amurense* habitat

From 1980 to 2020, the forest, grassland, waters, and unused land in the suitable habitat showed a downward trend, while cultivated and construction land showed an upward trend. The forest area decreased by 3.86% compared with 1980, mainly converted to cultivated land and grassland (**Figure 3C**). Notely, the conversion area gradually increased with the increase of years. Moreover, cultivated land and construction land increased by 12.80 and 36.32% compared with 1980.

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[6] https://www.helsinki.fi/

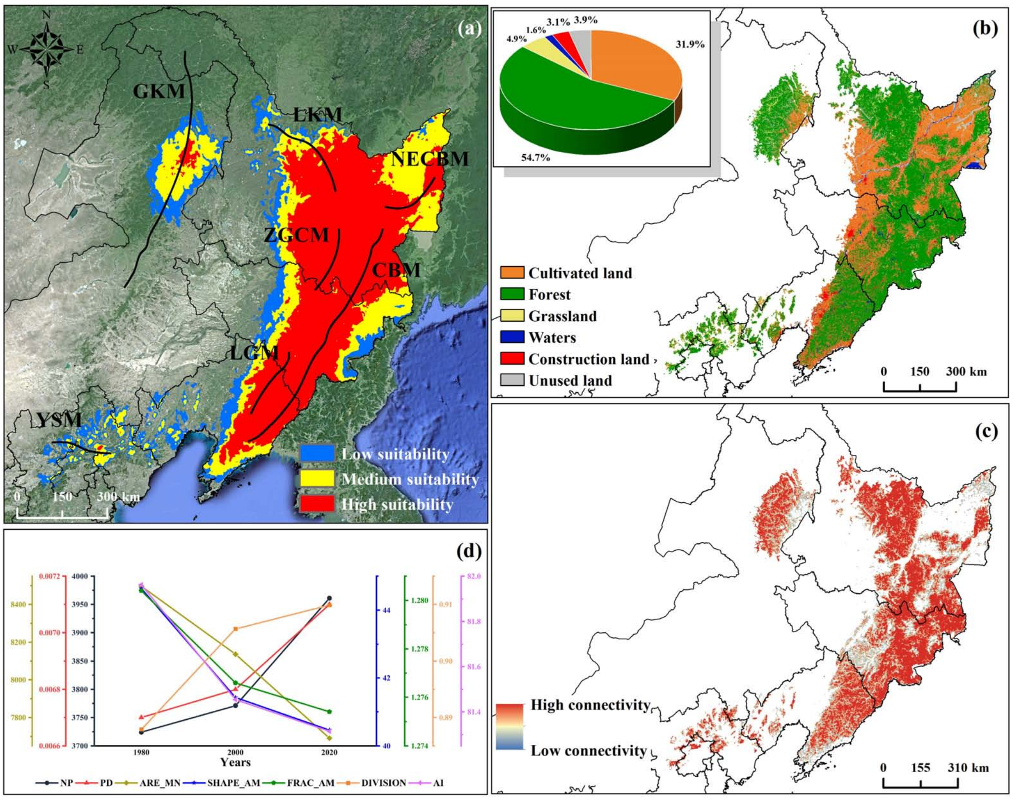

FIGURE 2
Distribution, land type, landscape fragmentation, and index change of suitable habitat of *P. amurense* under current climate conditions. **(a)** Distribution of suitable habitats of *P. amurense* under current climate conditions, of which abbreviations represents: GKM, Greater Khingan Mountains; LKM, Lesser Khingan Mountains; NECBM, North Extended Branch of Changbai Mountain; ZGCM, Zhang Guangcai Mountains; CBM, Changbai Mountains; LGM, Longgang Mountains; YSM, Yanshan Mountains. The distribution of mountain ranges has been improved from Wang et al. (2004); **(b)** Land use types of current potential distribution; **(c)** The landscape connectivity of the forests in the current potential habitat of *P. amurense*; **(d)** Change of landscape index of suitable areas in 1980, 2000, and 2020.

In the forest suitable for the survival and development of population, the average value of habitat quality decreased from 0.53 in 1980 to 0.51 in 2020, showing a downward trend (**Supplementary Table 5**). Among them, the area of high-quality habitat showed a downward trend in the past 40 years. The area of high-quality habitat in 1980 was about 29.43 × 10^4 km^2, and the area of high-quality habitat in 2000 and 2020 decreased by 4.23 and 5.30%. The medium and low-quality habitats area rose by 17.37 and 5.04% by 2020 (**Figure 3B**; **Supplementary Table 5**). Presently (2020), the areas with the high-quality habitat of *P. amurense* are mainly distributed in the central and southern parts of the Greater Khingan Mountains, the Lesser Khingan Mountains, and the forest areas of the Changbai Mountains. Moreover, the areas with medium-quality habitat are mainly concentrated in the forest landscape fringe. The areas with low-quality habitat are mainly cultivated land, grassland, construction land, rural residential land, waters, and unused land (**Figure 3A**).

3.3. Distribution changes under future climate conditions

Compared with the current climate conditions, the suitable area of *P. amurense* shows an increasing trend in the early stage of future climate change (2030s and 2050s). However, it would gradually decrease with the increase of years and carbon emissions in the 2070s and 2090s of high carbon emissions (SSP3-7.0 and SSP5-8.5). In all climate scenarios, the suitable area of *P. amurense* was the largest (68.25 × 10^4km^2) in 2050s-SSP3-7.0 scenario, and in 2090s-SSP5-8.5 scenario, the total area of suitable area is the smallest (46.59 × 10^4km^2). With carbon emission concentration increasing, the high suitability area of *P. amurense* would decrease gradually, while the low suitability area would gradually increase. Moreover, this trend gradually increases over the years (**Supplementary Figure 1**). Under 2090s-SSP5-8.5, the high suitability area would shrink to the minimum (12.21 × 10^4km^2), which decreases by 59.22% compared with the current potential high suitability area. Moreover, under 2090s-SSP2-4.5, the low suitability area would expand to 19.49 × 10^4km^2, with a change rate of 96.90% (**Supplementary Table 6**). The changing trend of the medium suitability area is the same as the total suitability area and the minimum area under 2090s-SSP5-8.5, about 17.16 × 10^4km^2.

In the future, the suitable area would mainly expand to the northwest of the Lesser Khingan Mountains, the north of the Greater Khingan Mountains, and the Hulun Buir Plateau. The suitable area would decrease mainly in the north of Yanshan Mountains, the south of Changbai Mountains, and the North extension branch of Changbai Mountain. These trends

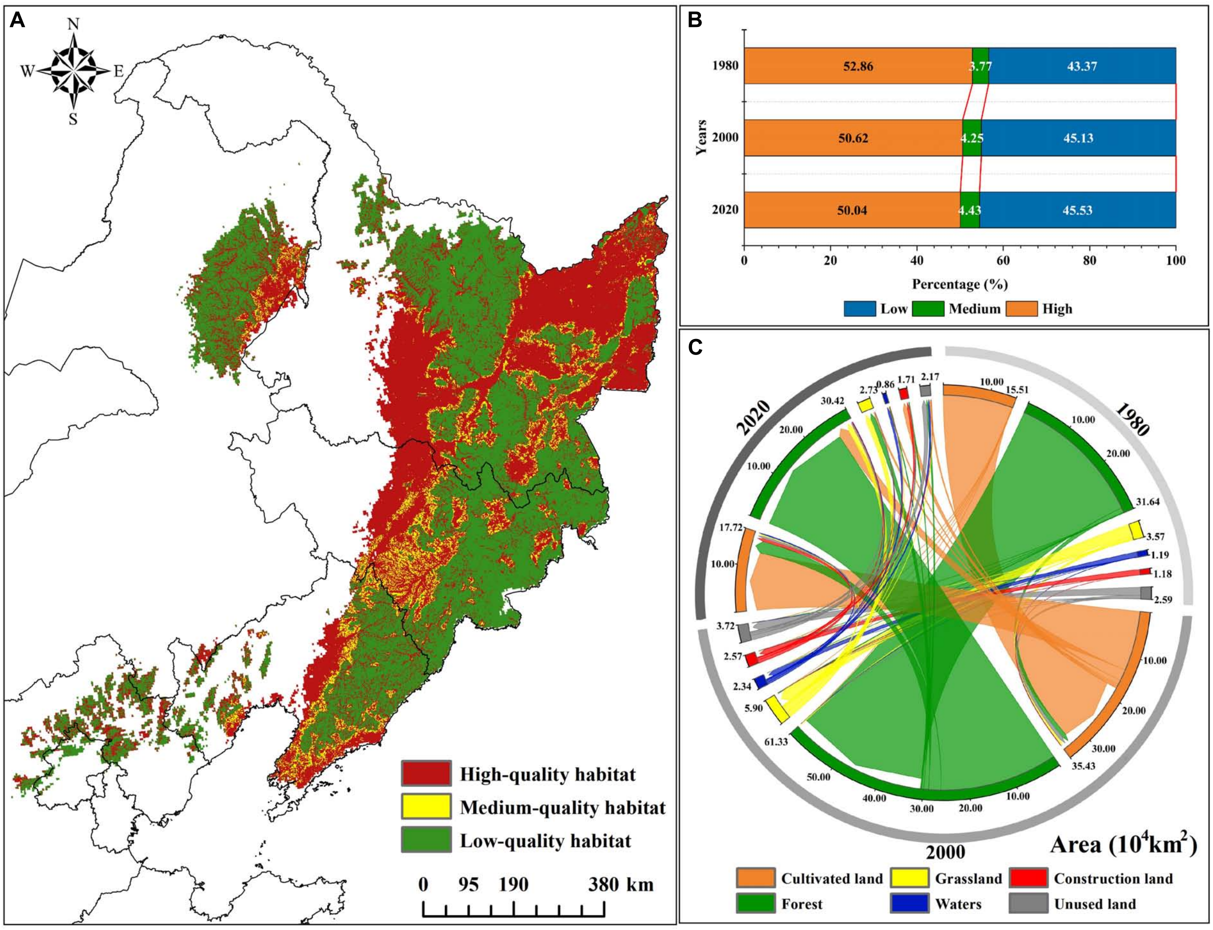

FIGURE 3
Habitat quality and land use change of current potential distribution of *P. amurense*. **(A)** The habitat quality of the current potential distribution; **(B)** Change of habitat quality area of different levels in 1980, 2000, and 2020; **(C)** Conversion area of land use type in 1980, 2000, and 2020.

expand gradually with the increase of years and carbon emission concentration (**Figure 4**; **Supplementary Figure 2**). Currently, the geographical coordinate of the *P. amurense* suitable area's centroid is 127.04°E and 44.97°N. It is predicted that under the 2090s-SSP3-7.0, the centroid would be shifted as far as the hill region between the southern foothill of the Lesser Khingan Mountains and the Songnen Plain (**Supplementary Figure 3**). Among 16 future climate scenario combinations, the centroid migration direction of suitable area is generally the same, and all move to the northwest direction of high latitude (**Figure 5**; **Supplementary Figure 3**). Meanwhile, with the increase of year and carbon emission concentration, the elevation of the centroids in the suitable area also increase gradually (**Figure 5**).

3.4. Main environmental variables affecting the distribution of *P. amurense* and their correlation with chemical composition

Among the eight environmental variables, Bio04, Srad08, Bio10, Bio11, Srad06, and Bio18 are the most important environmental factors affecting the distribution of *P. amurense* (**Supplementary Table 7**). The suitable ranges of the main environmental factors in *P. amurense* are shown in **Supplementary Table 8**. Among the suitable range of Bio04 is 1168.72 to 1617.71, the range of Srad08 is 15641.80 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ to 18968.08 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, Bio10 ranges from 16.74 to 23.24°C, Bio11 ranges from −20.70 to −6.44°C, Srad06 ranges from 18276.53 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ to 22818.40 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, the lowest value of Bio18 in this range is 294.63 mm and the highest value is 563.24 mm. With the increase of year and carbon emissions, climate factors in the current potential distribution would change (**Supplementary Figure 4**; **Supplementary Table 9**). Under the 2090s-SSP5-8.5, Bio10, and Bio11 would increase significantly, and the average value would increase by 5.43 and 7.39°C, respectively. Bio18 would increase slightly (+71.30 mm). While Bio04 would decrease significantly, the average decrease from 1438.28 to 1350.45 (**Figure 6**).

The results showed that Berberine is positively correlated with Bio18 and Srad10 (p-value < 0.01). The relationship model between Berberine and environmental factors is established as $C = 0.4055 \times \text{Bio18} + 0.6277 \times \text{Srad10}$; Palmatine content is positively correlated with Bio11 (p-value < 0.01), negatively correlated with Srad08 (p-value < 0.01), and negatively correlated

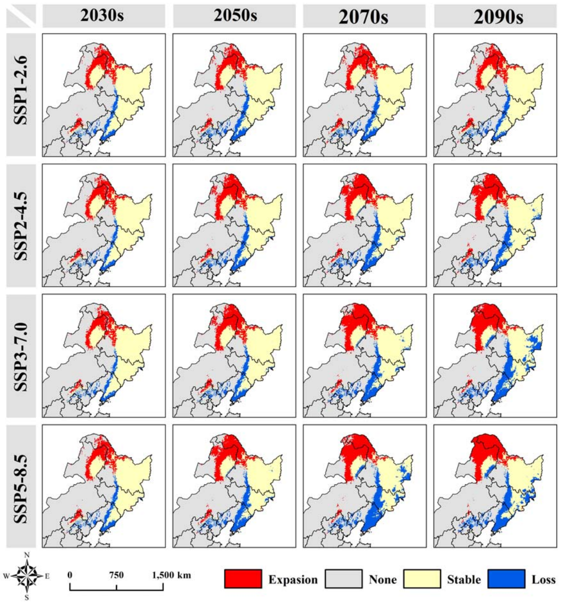

FIGURE 4
Spatial pattern changes of *P. amurense* under different climatic scenario combinations.

with Srad10 (p-value < 0.05). Moreover, the relationship model between Palmatine and environmental factors is established as $C = 1.9860 \times \text{Bio11} - 0.5745 \times \text{Srad08} - 1.3210 \times \text{Srad10}$ (Figures 7C, D; Supplementary Table 10). Currently, the spatial distribution of Berberine and Palmatine contents in the bark of *P. amurense* is shown in Figures 7A, B. The content of Berberine is higher in Hebei Province, northern Beijing, Liaoning Province, and southern and eastern Jilin Province. The content of Palmatine is higher in eastern and southern Heilongjiang Province, northeastern Jilin Province, and eastern and southern Liaoning Province.

3.5. Priority protection area and wild tending area for *P. amurense*

The priority protection area under the influence of future climate is about 7.66 × 10^4km^2, accounting for 13.77% of the current potential suitable area. The high and moderate protection areas are about 1.91 × 10^4km^2, and the high protection area is mainly distributed in the southeast of the Lesser Khingan Mountains, the middle of the Greater Khingan Mountains, and the Zhangguangcai Mountains (Figure 8A). The area of existing nature reserves in the *P. amurense* priority protection area is about 0.46 × 10^4km^2, covering 6.01% of the priority protection area. Specifically, the nature reserves in the low protection area are the most, about 0.32 × 10^4km^2. Moreover, the moderate and high protection areas are about 0.08 × 10^4km^2 and 0.07 × 10^4km^2 (Supplementary Table 11). Among the existing nature reserves, Red Pine Forest National Forest Park contains the largest area of moderate protection areas. Jinlongshan National Forest Park contributes the largest area of high protection areas. Furthermore, Dabane Wetland National Nature Reserve has the largest low and total protection areas (Figure 8C; Supplementary Table 12).

The wild tending area of *P. amurense* is mainly distributed in the Changbai Mountain and Lesser Khingan Mountains, with a small amount of distribution extending from the southern of Lesser Khingan Mountain range to the southern of Changbai Mountain Range and the central and southern of Greater Khingan Mountains (Figure 8B). According to the results of the spatial distribution of chemical constituents, the high-quality wild tending area of *P. amurense* is mainly distributed in the south and east of the Changbai Mountain. We analyzed the hot spots of high-quality wild tending areas in the county-level administrative units in China. The results showed 13 counties suitable for planning high-quality wild tending areas, such as Fengcheng County and Tonghua County (Figure 8D; Supplementary Figure 5).

4. Discussion

4.1. Main environmental factors affecting the distribution of *P. amurense* and their correlation with the content of chemical components

The predictors related to temperature are the main factors affecting habitat suitability for most tree species (Liu et al., 2022). The results of this study showed that the most important environmental factor affecting the distribution of *P. amurense* is temperature seasonality (Bio04). Bio04 is an index to measure the temperature change in a year and can represent the stability of climate (O'donnell and Ignizio, 2012). Since the duration of sunshine and the solar incidence angle do not change significantly throughout the year, the seasonal variation of temperature in tropical and temperate regions close to the equator is narrower than that in subtropical or temperate regions, so the seasonal variation in high latitude regions is obvious (Tagliari et al., 2021). The potential habitat of *P. amurense* in China is mainly distributed in high latitudes, which is also the reason for the high Bio04 value (1168.72∼1617.71) in the current habitat of *P. amurense*.

Bio11, the mean temperature of the coldest quarter, is another important environmental factor affecting the distribution of *P. amurense*. In general, winter temperature affects trees' growth rate in the following year. If the temperature is too low this season, the dehydration of protoplasm in the plant leaf cells or soil freezing will cause tree roots to freeze to death. Consequently, it will reduce photosynthesis in the next year and shorten the growth period of trees, which is not conducive to the growth of trees (Yuan and Li, 1999; Wang et al., 2003). Under climate warming, the inter-seasonal temperature difference in the suitable growth area of *P. amurense* gradually decreases, and the average temperature in the coldest month gradually increases, leading to the warming winter in the suitable area. The growing season of *P. amurense* in the next year may be extended with decreasing inter-seasonal temperature differences. Moreover, the prolonged growing season will accumulate more energy for the individual growth of the next year, which will accelerate its radial growth in the next growing season. Therefore, the rising temperature will positively affect survival and reproduction in the middle of this century. However, the seasonal temperature in the suitable habitat will decrease from 1438.28 to 1350.45, whereas the average temperature in the coldest

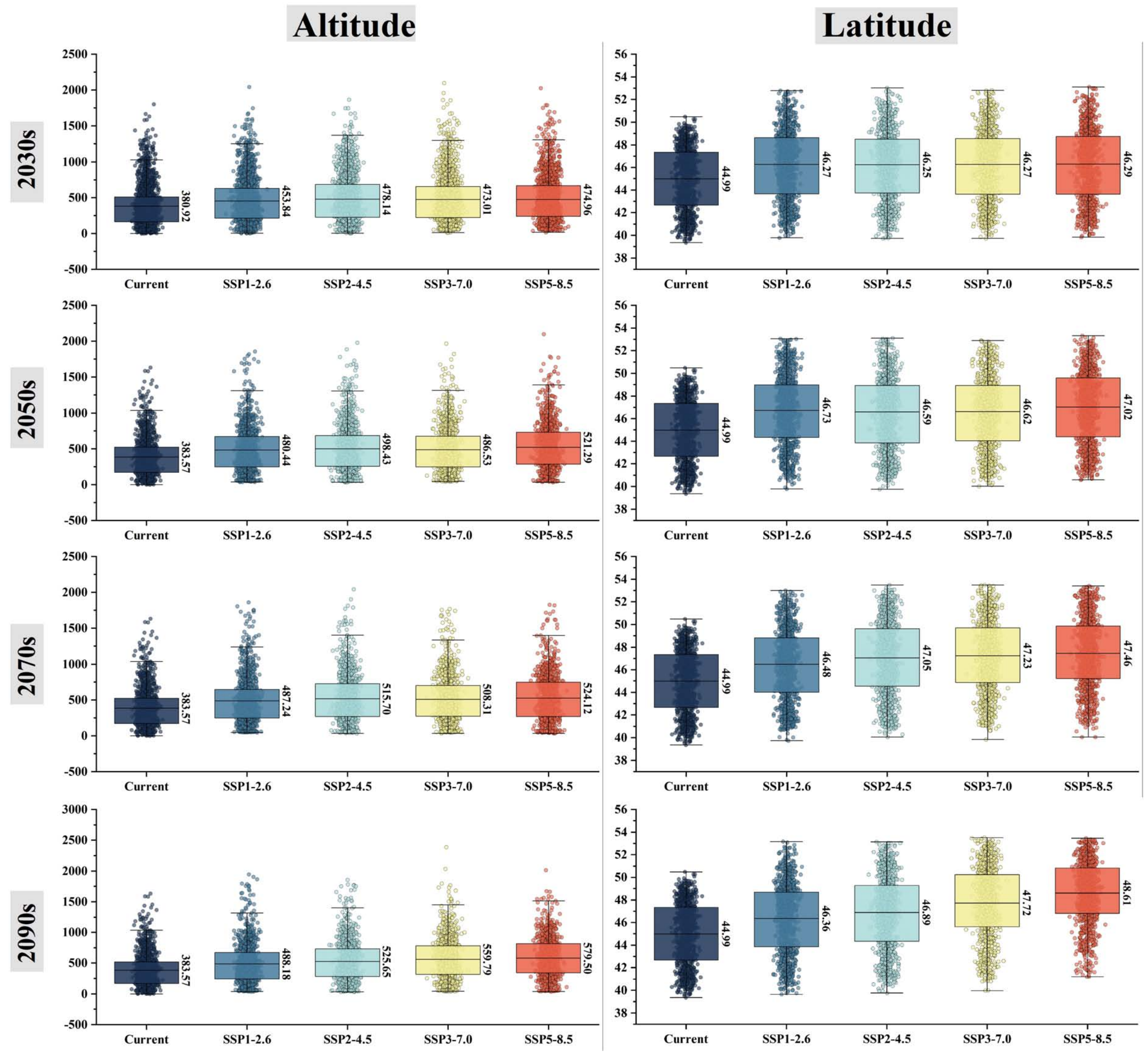

FIGURE 5
Spatial changes of altitude and latitude of the suitable areas for *P. amurense* under future climate combination.

month will increase by 7.39°C at the end of this century. It is worth noting that when the temperature in winter is too high, the respiration and metabolism of trees will be strengthened. The consumption of nutrients stored in the body for the next year's growth will be accelerated, harming the next year's growth and population fertility of trees (Edwards and Hanson, 1996; Cherubini et al., 1997). Therefore, the population of *P. amurense* will be further threatened at the end of this century due to the gradual increase of temperature increase in winter and the sharp reduction of the area of high suitability area.

Bio10 and Bio18 are also the main environmental factors affecting the distribution of *P. amurense*. Bio10 and Bio18 represent the mean temperature and precipitation in the warmest quarter of the year (O'donnell and Ignizio, 2012). The warmest quarter in Northeast China is from June to September, which is also the growing season of tree species in northern China (Li et al., 2017). The increasing lowest temperature in the growing season is conducive to extending the growth period of trees. During this period, appropriate precipitation will accelerate the accumulation of photosynthetic products and late growth (Liang et al., 2001). By the end of this century, the temperature and precipitation in the growing season in the suitable area will increase by 5.43 and 71.30 mm compared with the current. *P. amurense* needs sufficient water in the growing season, and the more adequate soil moisture, the better plant distribution (Huang et al., 2017). With the increase of temperature in the growing season, when the precipitation is appropriate, the negative impact of the decrease of forest soil water content caused by the increase of temperature on *P. amurense* and the positive demand of *P. amurense* for precipitation may reach a balance in some cases. However, when the balance is destroyed, and water stress is formed, it may limit the physiological and metabolic activities and inhibit its radial growth. Therefore, the "warm and dry" summer caused by climate warming will harm *P. amurense* over time.

Solar radiation profoundly impacts plant growth, development, and geographical distribution of species due to its different light

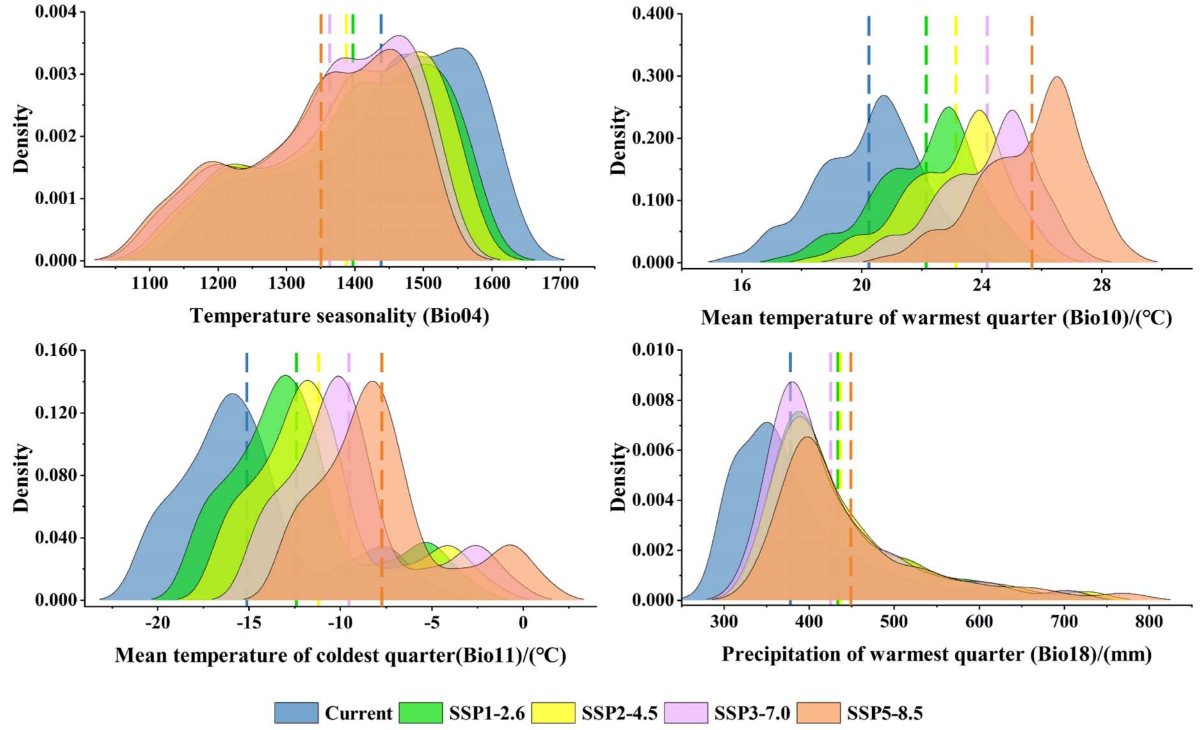

FIGURE 6
Density maps of key environmental factors under different climate scenarios in the 2090s.

intensity, light quality, and light period in different times and spaces (Li, 2017). Therefore, we included solar radiation factors in the species distribution model in this study. The results showed that these factors (Srad08, Srad10) are also important environmental variables affecting *P. amurense*. Since there is no matching future scenario with solar radiation data, in this study, solar radiation data exists in the species distribution model as a static variable. Some studies have pointed out that it is better or not worse to include static and dynamic variables in the species distribution model than to cover up or exclude static variables (Stanton et al., 2012). Therefore, the solar radiation data in our species distribution model improved performance for the present distribution. In conclusion, in the future climate change, the main environmental changes facing *P. amurense* population are warming in the cold quarter, the decrease of the temperature difference between seasons, and the warming and drying of the climate caused by the increase of temperature in the growing season.

Population chemical characterization manifests plant intra-specific diversity, which is significant for evaluating and utilizing medicinal plant germplasm (Zhang et al., 2016). The formation and accumulation of active components in *P. amurense* are determined by its genetic characteristics and are closely related to its surrounding ecological environment. Water and light factors have the most extensive impact on the active components of *P. amurense* (Zhang, 2015). The results of this study indicate that the most important environmental factor affecting the content of Berberine and Palmatine in *P. amurense* is solar radiation. The content of Berberine increases with the increase of solar radiation, while the content of Palmatine decreases with the increase of solar radiation. As Berberine is not the final product of secondary metabolism, it will be further converted into Palmatine and Jatrorrhizine (Gao et al., 2009; Huang et al., 2017), which makes the content of Berberine and Palmatine as well as the Jatrorrhizine present a complementary state, which may be the reason for this phenomenon. In addition to solar radiation, the environmental factor that affects the content of Berberine is precipitation, with a significant positive correlation between its content and precipitation. Another environmental factor that affects the content of Palmatine is temperature, which has a significantly positive correlation with temperature. Through constructing the spatial distribution layer of chemical components, we found that the areas with a high accumulation of active components of *P. amurense* are northeast Liaoning and southeast Jilin. This area is south of the current distribution, with sufficient light, warm temperature, abundant precipitation, and high annual active accumulated temperature. These results will provide a theoretical basis and important reference for the layout of production areas.

4.2. Spatial transformation characteristics of habitat of *P. amurense* under climate change scenario

In this study, Biomod2 is used to predict the *P. amurense* in China, and the results are consistent with most studies. It shows that the suitable habitat of *P. amurense* is mainly distributed in northeast China (Zhu, 1989; Chen, 2011). Our results showed that the Greater Khingan Mountains and the Yanshan Mountains in northern Hebei are only partially distributed, and Shandong, Shanxi, and Henan provinces are not distributed. It is worth noting

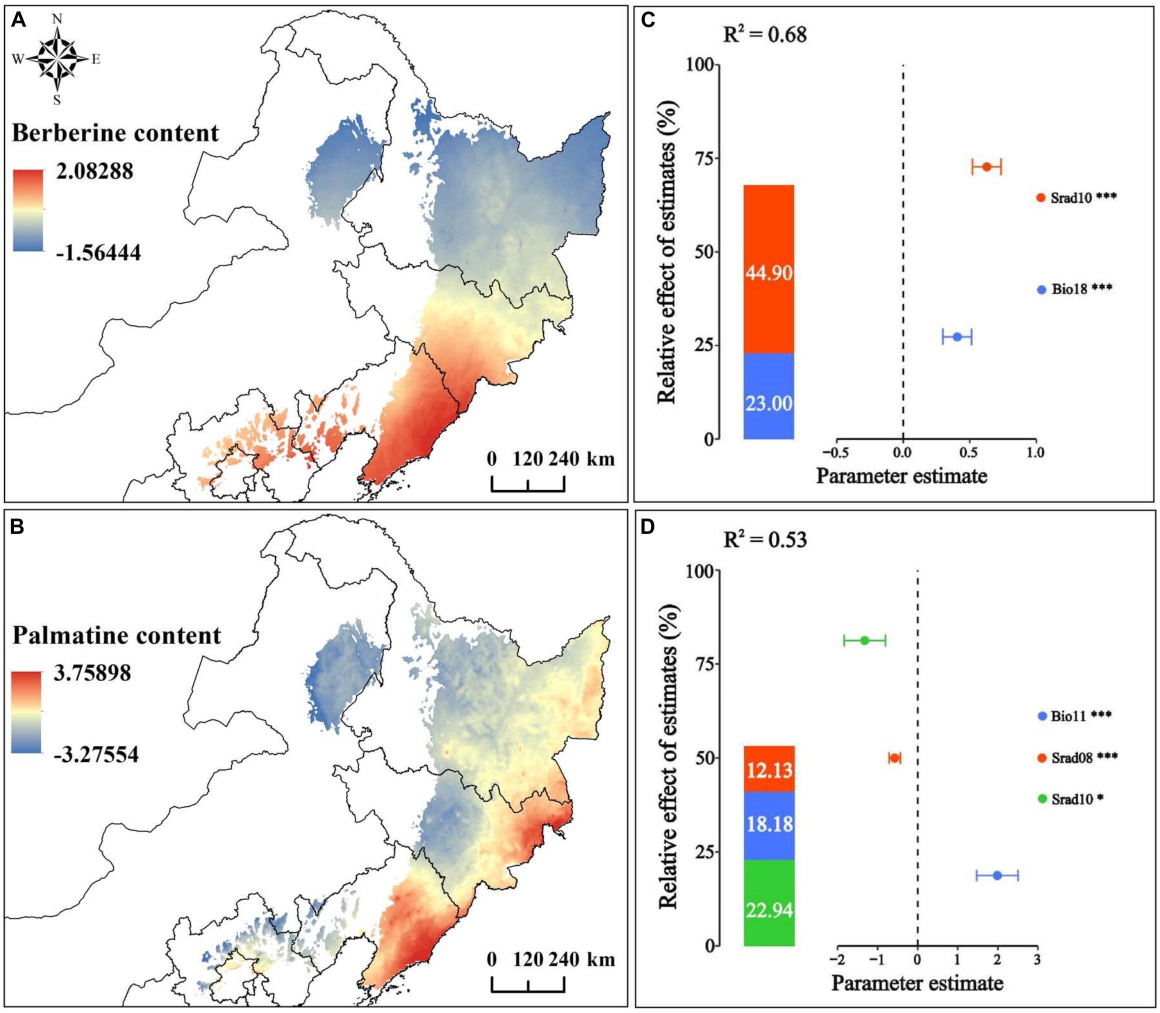

FIGURE 7
Correlation and spatial distribution of chemical composition and environmental factors of *P. amurense*; **(A)** Berberine spatial distribution; **(B)** Palmatine spatial distribution; **(C)** Correlation between Berberine content and environmental factors; **(D)** Correlation between Palmatine content and environmental factors. ***, **, and * represent the significance level of 1%, 5%, and 10% respectively.

that these results are not completely consistent with the results predicted by Huang et al. (2018). They were using the MaxEnt model. The Biomod2 model uses a variety of modeling techniques and integrates the results obtained by each method, which can reduce the deviation caused by the instability of a single model and can more accurately predict the range of suitable habitat of *P. amurense* (Araújo and New, 2007; Goldsmit et al., 2020).

In the future climate scenario combination, except for the 2090s-SSP5-8.5, the suitable area of *P. amurense* shows an increasing trend compared with the current. However, the increasing range of area decreased yearly with the increase of carbon emissions. Spatially, the change in the suitable area of *P. amurense* is consistent with most species' migration direction (Li et al., 2019), and the general distribution area gradually moves to the northwest high latitude and high altitude area. In the future, the suitable area of *P. amurense* will expand to the northern forest of China, mainly located northwest of the Lesser Khingan Mountains and north of the Greater Khingan Mountains. The temperature difference between day and night in the expansion is large, and the extreme temperature can reach below −40°C (Ma, 2021), which exceeds the semi-lethal temperature of the isolated branches of *P. amurense*. Therefore, this region is not suitable for the growth of *P. amurense*. Projections of future climate scenarios indicate that northern forest temperatures will change more dramatically than the global average trend, with winter temperatures in northern forests projected to increase by 40% over the global average by 2,100 (Han and Wang, 2016). As the temperature rises, similar climatic conditions will be formed in this region as in the current *P. amurense* growing area. The current potential distribution of *P. amurense* is in the subhumid and humid regions. Under different combinations of future climate scenarios, the expansion is also in subhumid and humid regions. The soil moisture content in the expanded regions could still meet the growing demand for *P. amurense*. Therefore, the temperature change is the main reason affecting the dynamic change of distribution pattern of *P. amurense*.

The disappearance area of the suitable habitat is mainly distributed in the north of Yanshan Mountains and the south of Changbai Mountains. This region is mainly located in the subhumid region and the border region between subhumid and humid in northern China. Under future climate change, most of the

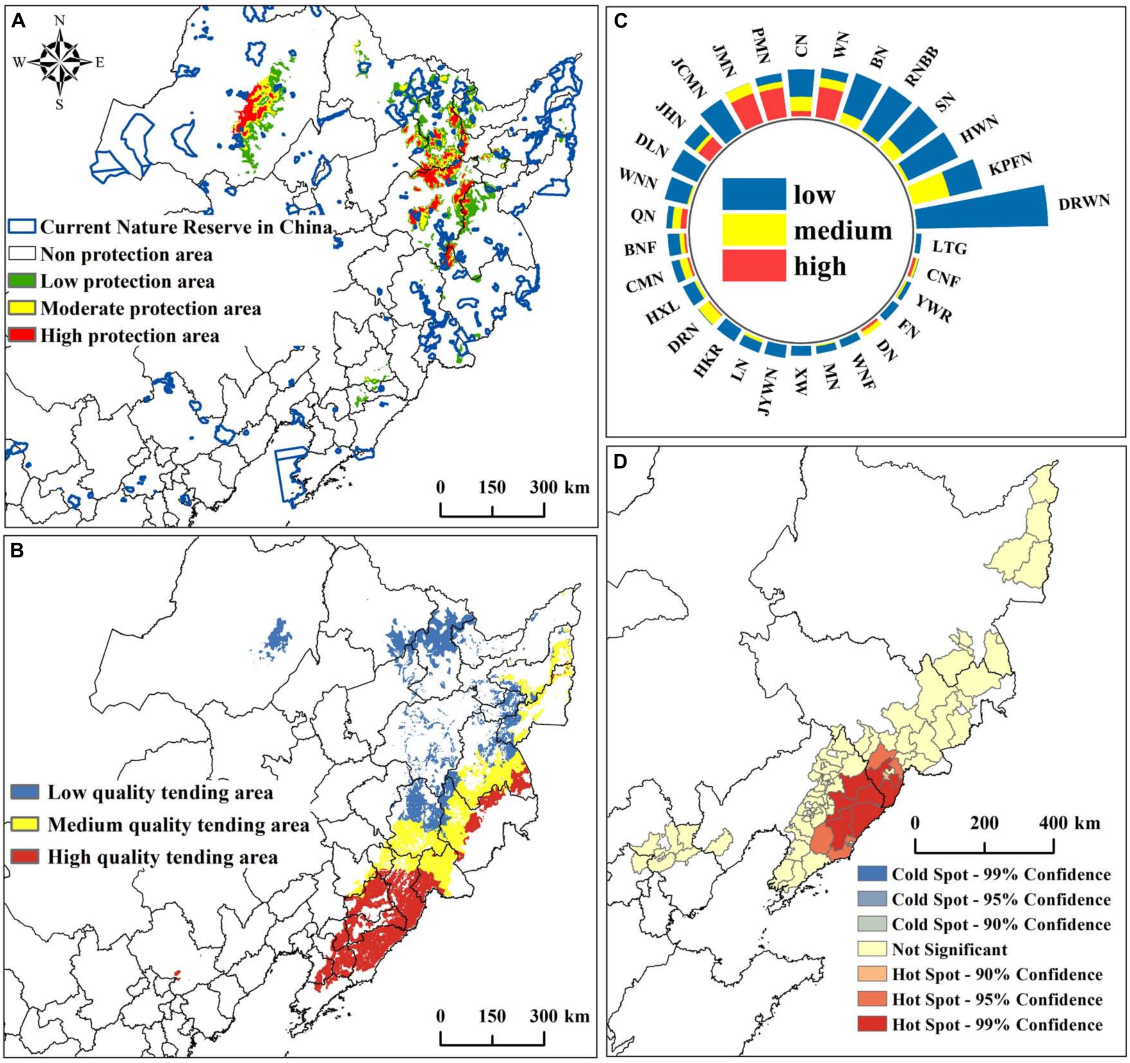

FIGURE 8
Prediction results of *P. amurense* reserve and wild tending. **(A)** Distribution of priority protection areas; **(B)** Distribution of different quality wild tending areas; **(C)** The area of each grade of priority protection areas within the existing nature reserve; **(D)** Hotspots analysis at the county level in high-quality wild tending areas.

humid areas in northern China will be transformed into subhumid areas, the overall humid areas will shrink, and the subhumid and semi-arid areas will expand to the east (Ma et al., 2019). The warm and dry climate will reduce the moisture of surface soil and increase evaporation, resulting in a decrease of climate moisture index and not conducive to the absorption of soil fertility by plant roots (Michaelian et al., 2011; Peng et al., 2011). The area in the subhumid and the suitable area's boundary are no longer suitable for *P. amurense* due to this climate. Therefore, warming and drying caused by global warming is the main reason for reducing the suitable area of *P. amurense*.

In addition to temperature limiting plant growth, poor soil and nutrition also limit plant growth (Lafleur et al., 2010). In the global warming, the permafrost in the Greater Khingan Mountains and Lesser Khingan Mountains in Northeast China has experienced significant warming and degradation (Jin et al., 2009). In the 21st century, the active layer thickness of permafrost in the northern forest area may increase by 5~30 cm every 10 years (Hayes et al., 2014). This phenomenon will accelerate the release of permafrost nutrients and promote the decomposition of soil organic matter, thus improving the barren soil and nutrient deficiency (Han and Wang, 2016). Therefore, we speculated that the increase in soil nutrients provides the basis for migration. It is worth noting that the temperature and soil temperature in the northern forest area shows contradictory responses to climate change based on the complexity of interactions between soil, landscape factors, and climate change. The sensitivity of this region to temperature is far greater than that of other biotas. With climate warming, the structure and function of the northern forest ecosystem tend to deteriorate, and its composition tends to be simple (Hennon et al., 2012). Therefore, in the future, we should strengthen the study of *P. amurense* population, community, landscape, and other aspects with multi-method and multi-scale coupling. At the same time, long-term field positioning observation and indoor simulation experiments are combined to increase the accuracy of model inference.

It is worth noting that the complete ecological niche models should be more reliable, because they are calibrated with a much higher number of presences and capture a much wider range of occupied environmental conditions (Pearson et al., 2004). However, without enough bias-free regional data, we cannot objectively identify the actual improvement of regional models after incorporating information from the global niche (El-Gabbas and Dormann, 2018). Through the network database and literature review, since the middle of the 20th century, the occurrence data of *P. amurense* outside the study area (China) is very little. And in the record of the literature, there are still areas [Korea (Democratic People's Republic of)] did not search the occurrence data. Meanwhile, SDM that rely on regional-scale environmental variables will play a key role in forecasting species occurrence in the face of climate change (Requena-Mullor et al., 2019). Therefore, this article has conducted a regional species distribution modeling based on China as the research scope, which can still provide a reasonable explanation for the distribution pattern of suitable habitats for *P. amurense* in China in the context of climate change.

4.3. Impact of habitat and landscape pattern changes on the distribution of *P. amurense*

There are two main forms of habitat fragmentation: (1) Morphological fragmentation is caused by the reduction of habitat area and the enhancement of edge effect caused by human activities. Habitat fragmentation leads to habitat fragmentation of species. (2) Ecological function fragmentation is caused by the reduction of species' adaptability to habitat due to climate change (Ran et al., 2019). From 1980 to 2020, the forest landscape area in the suitable area of *P. amurense* was gradually transferred to cultivated land, grassland, construction land, and unused land. Cultivated land was the main transfer direction, and the area increased yearly. In addition, with the decrease in forest area, the habitat quality of *P. amurense* decreased year by year, and fragmentation gradually intensified. It can be seen that the main reason for habitat quality and pattern changes in the past 40 years is human activities.

Interannual changes in climate are normal. Even in the absence of long-term climate change, most species tolerate such short-term climate changes by changing the functional shape of plants through climate-related genetic variation in natural populations (Fridley and Grime, 2010; Wang et al., 2020). For plants, better interspecific gene exchange can improve adaptability, increasing species and population size (Reed and Frankham, 2003; Wan et al., 2014). Habitat fragmentation will affect genetic drift, intensify inbreeding and reduce the gene flow of the population, thus posing a threat to the population, as well as affecting the number of species in the community and the ability to cope with environmental disturbances such as outbreaks of pests and diseases and extreme weather events (Jump and Peñuelas, 2005). *P. amurense* population has low genetic diversity and no obvious genetic pattern (Wang et al., 2014). As a traditional Chinese medicine, the bark of *P. amurense* has been cut down and peeled for a long time, resulting in the gradual fragmentation of its habitat, the gradual reduction of the population size, and the formation of small, isolated populations. The smaller population and lower population density will not only reduce the genetic variability of *P. amurense*, which may lead to more and more obvious genetic drift and inbreeding decline, but also bring inconvenience to insect pollination, resulting in small gene flow among *P. amurense* populations (Yan et al., 2006). The size of plant gene flow largely depends on how the plant reproduces and how the propagules move. For seed-mediated gene flow, pollen gene flow is dominant, and the dispersal and distribution mechanism of plant pollen is an important factor in determining the genetic structure between populations, among which wind-pollinated plants have higher gene flow than animal-pollinated and self-pollinated plants (Wen et al., 2010). As an insect flower, the gene flow of *P. amurense* is small. In addition to genetic drift and gene flow, the breeding system also greatly impacts genetic diversity. After maturity, *P. amurense* seeds mostly fall around the mother. However, allelopathic substances that exist in the peel and fallen leaves of mother plants can effectively inhibit seed germination (Zhang et al., 2011; Dai et al., 2012). Moreover, the plant community has high shade, many fallen leaves on the ground, and a deep dormancy mechanism. These factors restrict germination and the growth of seedlings. At the same time, the genetic information carried by seeds has a slow transmission speed and a long transmission period, which reduces the gene exchange frequency and decreases genetic diversity in the wild population (Wang et al., 2014). Therefore, the reduction of genetic diversity in the population of *P. amurense* may reduce the population's tolerance and recovery ability under the interference of future climate change.

However, for both individuals and species, adaptation to environmental changes through phenotypic plasticity is limited. Moreover, changes in the distribution of species are inevitable when climate change exceeds what plants can tolerate (Bradshaw, 1965; Bradshaw and McNeilly, 1991). As the climate warms, individuals in the population may move to higher altitudes and latitudes to respond to the movement of its best climate (Jump and Peñuelas, 2005). Migration usually occurs across the species range in the form of propagules and pollen dispersal rather than simply due to the expansion and contraction of range edges (Davis and Shaw, 2001). The long-distance transmission of the seeds of *P. amurense* mainly depends on fruit-eating animals, but habitat fragmentation will reduce the diversity of fruit-eating animals. In the past 40 years, the forest land in the suitable habitat has been gradually fragmented. If not controlled, the suitable habitat will be seriously fragmented in the future, which will not be conducive to the spread of seeds and pose a threat to the survival of the population. Therefore, if the reduction degree and fragmentation degree of the habitat area of *P. amurense* is further intensified in the future, a few individuals can survive in the landscape for a long time. However, it will lose the ability to maintain a stable population, which may form the "living dead population" (Chen et al., 2022).

The main causes of species endangerment are habitat destruction, environmental pollution, habitat degradation, and overuse of biological resources (Lande, 1988). With the increase in economy, urbanization, and agricultural development, human development and utilization of the land gradually occupy a leading position. If we continue to develop the land according to the trend of land use change in the past 40 years, the habitat of *P. amurense* will be seriously destroyed at the end of this century. In addition, without human intervention, it is very difficult to form seedlings and increase the population of individuals since the natural habitat is not conducive to the self-renewal of the *P. amurense* population. Therefore, it is suggested to focus on forest vegetation restoration projects and identify priority protection areas and high-quality wild tending areas in *P. amurense* suitable areas. These actions can better protect the wild resources and reasonable development and utilization.

4.4. Priority conservation area and high-quality wild tending area of *P. amurense*

As an important tree species for traditional Chinese medicine, *P. amurense* is threatened due to its extensive and illegal harvest (Yu et al., 2013; Wan et al., 2014). In the past 20 years, the destruction of wild resources of *P. amurense* has been restrained to a certain extent due to the change in the national forest management mode and the strengthening of the protection of endangered species (Zhang et al., 2016). However, our results showed that upper climate change would seriously threaten the distribution of *P. amurense* in the absence of anthropogenic disturbance. Moreover, its population renewal ability is weak, which is not conducive to the improvement under threat (Zhang et al., 2016). These troubles may lead to the shortage or loss of local medicinal resources of *P. amurense*. Wild cultivation is an effective way to solve the gap between the supply and demand of medicinal plants. However, a major premise of medicinal plant cultivation is to ensure high-quality medicinal materials (Shen et al., 2021). Given this, it is important to integrate climate change and land use landscape patterns for planning suitable protection areas and wild tending areas of *P. amurense*.

Based on climate change and landscape patterns, this study determined the priority protection area of *P. amurense* in China. Although there are some national and provincial nature reserves within the range of *P. amurense* suitable area, our results showed that the existing reserves only contain 6.01% of the priority protection area under future climate change. There is still a large area that has not yet been protected. Among the existing nature reserves, Jinlong Mountain National Forest Park has the largest area of high protection areas. The climate conditions are highly suitable and will not change significantly in the next century, and the species will be less affected by climate change in the reserve. Therefore, in this century, Jinlong Mountain National Forest Park may contribute to the protection of *P. amurense*. We believe that the protection of *P. amurense* should be carried out in the southern part of the Lesser Khingan Mountains and the northern part of the Changbai Mountains. There is no potential climate pressure under future climate, and the forest is relatively concentrated, which is conducive to gene exchange between the populations.

Phellodendron amurense can be harvested after planting for 10–15 years (Yan et al., 2013). According to China's national policy, it is forbidden to plant perennial woody medicinal materials and trees on cultivated land. Therefore, to promote the protection, recovery, and sustainable utilization of the population, it is necessary to carry out the related work of wild tending of *P. amurense*. The wild tending of traditional Chinese medicine achieves the coordinated development between producing medicinal materials and protecting the ecological environment. In this way, the sustainable renewal of the tending population of traditional Chinese medicine can better protect the rare and endangered medicinal materials and their biodiversity (Chen et al., 2004). In addition, the wild tending area is the original environment, with less human interference and far away from pollution sources, providing high-quality wild medicinal materials for medical treatment. At the same time, wild tending makes full use of the natural growth characteristics, reducing the cost of manual management and obtaining high returns with low investment. With wild tending being accepted and related research being carried out one after another, a new mode of ecological industry of traditional Chinese medicine will be opened.

This study plans a high-quality wild tending area based on the current forest area in high suitability of *P. amurense* and the distribution information of effective chemical components. In this way, we can effectively avoid the waste of investment caused by blind planting. According to the planning results, we put forward the following suggestions. (1) High-quality wild tending areas are mainly distributed in the south and east Changbai Mountain. It is important to note that most of this area is at high risk for habitat loss. Therefore, it is suggested to collect wild germplasm and evaluate its diversity. (2) The cultivation of *P. amurense* in the planned high-quality wild tending area should be combined with local policies, especially with the policies designated at the county level. Besides, integrate the ecological, economic, and social benefits of the mountain areas, and strengthen the establishment of the wild cultivation medicine base. These protective actions can regulate people's habit of plundering and digging wild medicinal materials and strengthen the protection of biodiversity and the ecological environment. Furthermore, the contradiction between resources and supply-demand, population renewal, ecological protection, and biodiversity of *P. amurense* will be effectively solved. At the same time, it is also necessary to strengthen the research on the base management mechanism and other aspects to ensure smooth operation and achieve the purpose of nurturing. (3) Mastering the basic characteristics of the growth and development of wild traditional Chinese medicine is the basis for determining their wild tending methods, reproduction, and growth. Moreover, the development and population renewal of the tending medicinal materials are affected by various environmental factors (Chen et al., 2004). Therefore, it is necessary to strengthen the research on developmental biology, population ecology, and wild tending methods of *P. amurense*. In the wild tending plan of *P. amurense*, the environmental factors that affect the content of its chemical components and their future changes should be emphatically considered so that the planned wild tending area of *P. amurense* has timeliness. (4) Strengthen the research on the possibility of other organs of *P. amurense* to be used as medicine, and change the single way of using the medicine. It is the fundamental way that solves the contradiction between protecting and utilizing *P. amurense* resources.

5. Conclusion

In the analysis of the change of the distribution range of *P. amurense* under the future climate in China, although climate warming will gradually reduce the area of the suitable habitat and move to the northwest, there is still a climate-stable area suitable for the growth of *P. amurense*. In the past 40 years, the habitat quality of the suitable habitat of *P. amurense* has decreased year by year, and the natural habitat has shown a trend of gradual fragmentation. Based on the above reasons, we constructed a protection framework for the rare and endangered medicinal material–*P. amurense*. (1): The forest areas in the middle of the Greater Khingan Mountains and the Lesser Khingan Mountains are climate-stable areas. Therefore, this area is regarded as the priority protection area of *P. amurense* to prevent the resources from being seriously damaged, even facing the crisis of extinction by climate change and human activities. (2): Based on the correlation between the content of chemical components and environmental factors, the wild tending areas of *P. amurense* were planned. Wild tending not only restores and increases the population, improves the habitat environment, and enriches the genetic diversity of the population but also ensures the sustainable utilization of wild medicinal plant resources, maintains the balance between the utilization of wild medicinal plants and the protection of the ecological environment, and realizes the harmonious coexistence of human and nature. This work is a targeted proposal for the protection of *P. amurense* and provides a reference method for the protection and utilization of other rare and endangered wild medicinal species. In the future, we will pay more attention to the long-term monitoring of environmental factors in the high suitability of the *P. amurense* population. Consequently, obtaining high-quality modeling parameters can provide a more scientific and accurate theoretical basis for protecting *P. amurense*. We conducted in-depth biological research on *P. amurense* and formulated reasonable and scientific wild tending methods in line with the policy prohibiting "non-grain cultivation" of cultivated land in China. Our results can alleviate self-renewal obstacles of the *P. amurense* population, effectively improve its ecological and economic value, and meet the rigid growth demand for high-quality traditional Chinese medicinal materials in the era of the global health economy.

Data availability statement

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

Author contributions

BZ: writing–original draft preparation, writing–review and editing, data curation, and software. HZ and XXZ: conceptualization, writing–review and editing, and methodology. BC: writing–review and editing. XYZ: investigation and validation. XK: data curation. CW: supervision and conceptualization. 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.2023.1186627/full#supplementary-material

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Identifying global research and conservation priorities for Columbidae: a quantitative approach using random forest models

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The family of Columbidae, including pigeons and doves, remains understudied despite their patrimonial value and high ecological and conservation relevance. Currently, 353 extant columbid species are listed in the IUCN red list, with about 20% of them being threatened with extinction. However, there has been little effort so far to synthetize the available information on factors influencing extinction risk and the allocation of research effort among columbid species. In this context, using random forest models, the present study aims at quantitatively assessing to what extent environmental, life history and socio-political factors may drive the extinction risk of pigeons and doves and explain differences in scientific attention among species. We found that high risk of extinction in columbids is associated with small historical range, exposure to invasive alien mammals and living in isolated islands and/or at low altitudes, while the probability of population decline is associated with species body size, surrounding human density and narrow habitat breadth. We also evidenced a large disparity between species or population extinction risk and scientific interest. Indeed, most of the studies on columbids have been conducted by scientists from North America and Western Europe on their local species, whereas species from biodiversity hotspots, which are more at risk of extinction, have comparatively received little attention. This unequal acquisition of knowledge creates gaps that deserve to be filled in order to have a good appreciation of extinction risk in columbids and associated threats, through fair transnational cooperation, academic training and regional coordination in conservation-oriented research on columbids.

KEYWORDS

biogeography, doves, endangered species, extinction risk, pigeons, scientific attention, threatened species

1 Introduction

The rate of biodiversity loss is currently increasing at an unprecedented rate, as a direct consequence of habitat loss, fragmentation and degradation, biological invasions, and climate change (Balmford et al., 2003; Barnosky et al., 2011). However, the extent and rate of biodiversity loss are not uniform around the globe (Howard et al., 2020), nor across taxa (Pimm et al., 2014). As available funding for conservation research and actions is limited (Evans et al., 2012; Waldron et al., 2013), there is an obvious need to define priorities for optimizing resource allocation (Brooks et al., 2006). Ideally, prioritization mechanisms should be based on sound and reliable scientific evidence (Williams et al., 2020). However, important gaps in knowledge still exist, particularly in several biodiversity-rich countries, such as Haiti or sub-saharan African countries, where ongoing conflicts, political instability and poor access to facilities and funding severely hamper the development of field research and monitoring programs (Hanson et al., 2009; Siddig, 2014; Conteh et al., 2017; dos Santos et al., 2020; Vallès et al., 2021). In addition to spatial bias, the conservation literature tends to give a disproportionate attention to emblematic, charismatic, and flagship species (Andelman and Fagan, 2000; Brambilla et al., 2013; Mammides, 2019; Habel et al., 2021). Consequently, there is a certain mismatch between research efforts and conservation priorities (Christie et al., 2021).

Avian conservation biology research is no exception to the rule (de Lima et al., 2011; Ducatez and Lefebvre, 2014; Murray et al., 2015; Roberts et al., 2016; Buechley et al., 2019). Various factors, such as environmental conditions, phylogeny, life-history traits, levels of anthropogenic pressure, or socio-political factors, independently or jointly, can affect the risk of extinction of avian species (Owens and Bennett, 2000). For instance, extinction risk is not distributed randomly among avian families and in relation to fecundity and body size (Bennett and Owens, 1997). On the other hand, the severity of extinction risk of avian species varies in relation to socioeconomic factors and human pressure (Olah et al., 2016; Chen et al., 2019). Similarly, variation in the level of scientific attention among bird species is significantly influenced by phylogeny, geographic range and ecological life history traits, with non-threatened species being studied twice as much as threatened ones (Ducatez and Lefebvre, 2014). For instance, although the Andean Flamingo, *Phoenicoparrus andinus*, is the least abundant flamingo in the world and is listed as Vulnerable by the IUCN Species Survival Commission (Derlindati et al., 2014), it has received far less attention than the Least Concern Greater Flamingo, *Phoenicopterus roseus* (Johnson and Cézilly, 2007; Geraci et al., 2012). In addition, the majority of avian conservation research is conducted in developed countries and/or by North American and western European researchers, confirming the mismatch between priorities and capacity for research and conservation (Brito and Oprea, 2009; Vallès et al., 2021).

In particular, Columbidae, the only extant family of Columbiformes, is particularly understudied, despite its patrimonial value and high ecological and conservation relevance (Walker, 2007; McKenzie and Robertson, 2015; Devenish-Nelson et al., 2019; Yarwood et al., 2019). Pigeons and doves are one of the oldest and most diverse extant lineages of birds. However, their evolutionary radiation and phylogeny remain poorly resolved (Soares et al., 2016), with the creation of new genus or species and the slimming of other genus based on molecular or paleontological evidence (Johnson et al., 2001; Banks et al., 2013; Sangster et al., 2018; Steadman and Takano, 2020). Currently, the family Columbidae includes about 370 species that are distributed on all continents, except for the high Artic and Antarctica (del Hoyo et al., 1997; BirdLife International, 2022). They occur in various habitats (del Hoyo et al., 1997; Gibbs et al., 2001; Carvalho et al., 2015; Fey et al., 2015; Monterrubio-Rico et al., 2016), where they provide important ecosystem services, particularly through seed dispersal (Meehan et al., 2005; Wotton and Kelly, 2012; Costan and Sarasola, 2017; Ando et al., 2021). However, a significant proportion of columbid species are endangered or threatened with extinction (Bennett and Owens, 1997; Walker, 2007; Rivera-Milán et al., 2015; Lees et al., 2021). This results in habitat fragmentation and degradation, introduced predators, competition with invasive columbid species, excessive hunting pressure and ineffective management, and trade (Walker, 2007; Carvalho et al., 2015; Camacho-Cervantes and Schondube, 2018; Lamelas-López et al., 2020; Lormée et al., 2020; Moreno-Zarate et al., 2021; Bacon et al., 2023). The conservation status of several species remains uncertain, mainly due to lack of data (del Hoyo et al., 1997; Walker, 2007). This is particularly true of secretive species or species with very restricted geographical range for which traditional study methods might not be appropriate (Cambrone et al., 2021). More to the point, little effort has been made so far to synthetize the available information on the factors influencing the conservation status of columbid species and research effort. To the best of our knowledge, only Walker (2007) provided a short review of the main drivers of extinction risk for columbid species based on a relatively simple statistical analysis of data available from BirdLife International, emphasizing the vulnerability of insular species. We went further in the present study by quantitatively assessing to what extent environmental, life history traits and socio-political factors may (i) drive the extinction risk of pigeons and doves and (ii) explain differences in scientific attention among species. To that end, we relied on random forest (RF) models and an updated database (including both IUCN conservation status and population trends of columbid species) especially compiled for this study.

2 Materials and methods

2.1 Database creation

2.1.1 Information about columbid species

We obtained data for the 369 species from three main sources: Birdlife international (BirdLife International, 2021), the website *Birds of the World* (https://birdsoftheworld.org) and *Pigeons and Doves: A Guide to the Pigeons and Doves of the World* (Gibbs et al., 2001). We extracted information on biological, ecological and environmental traits that are likely to influence extinction risk (see Buechley et al., 2019). We classified explanatory variables into four categories: “environment”, “behavior and life history”, "anthropogenic pressure" and "socio-political indicators" (Table 1). In order to estimate each species' extinction risk, we relied on IUCN Red List categories and global population trends (BirdLife International, 2021). We classified species as threatened (critically endangered *CR*, endangered *EN* and vulnerable *VU*), non-threatened (near-threatened *NT* and least-concern *LC*), extinct (extinct *EX* and extinct in the wild *EW*), or data deficient. Because non-threatened species do not necessarily show stable or increasing population trends (Figure 1), we used global population trends of species (Rodrigues et al., 2006) as a second proxy of extinction risk. Species were thus classified as increasing, stable or decreasing according to BirdLife International (2021).

2.1.2 Scientific attention

In order to quantify scientific attention given to each columbid species, we relied on the number of peer-reviewed articles retrieved from an extensive bibliographic search on all databases of the Web of Science (conducted by mid-2021). We performed searches using current and past binomial scientific names, vernacular names in English, French and Spanish and all recognized synonyms. To compile all possible names of species, we used the websites *Avibase* (https://avibase.bsc-eoc.org) and *Birds of the World*. We considered several "research areas", as defined in the Web of Science, as all studies bringing ecological knowledge about a species may be of help for its conservation (Courchamp et al., 2015). Each search was conducted using the following procedure:

"TS="
(in order to search following terms in title, abstract and
keywords of articles)
+
Full binomial scientific names, vernacular and all recognized
synonyms in independent quotes, separated by "OR"
+
"AND SU=("Ecology" OR "Biodiversity and Conservation"
OR "Ornithology" OR "Evolutionary Biology" OR "Zoology")"
(to limit searches to studies related to following
science disciplines: Ecology, Conservation Biology, Ornithology,
Evolutionary Biology/Ecology and Zoology)
+
"NOT SU=("Veterinary Sciences" OR "Neurosciences and
Neurology" OR "Anthropology")"
(to exclude any study related to veterinary sciences,
neurosciences and neurology, and anthropology).

We also performed a global search in order to estimate national contributions to research on Columbidae, assessed from the affiliations of authors of peer-reviewed articles. To that end, we used the same search nomenclature, except that we replaced names of species and their synonyms by "Columbidae", "Columbiformes", "Pigeon" and "Dove", separated by the Booleans operator "OR". In order to exclude all articles on Pigeon pea (*Cajanus cajan*), we added: NOT TS=("Pigeon*pea*" OR "*Cajanus cajan*").

2.1.3 Spatial analyses (GIS)

We used QGIS (3.10.11) to calculate spatial statistics for explanatory variables used in our analyses (Table 1 and Supplementary Material 1, Method A1). We obtained various raster and polygon files for historical species range from several sources (Table 1), and rasterized polygons representing area distribution of species using scientific attention (log[number of articles + 1]) as value for the raster unit (square of 400km^2). Since, polygons of several species may overlap, we beforehand calculated the mean of scientific attention per raster unit.

2.2 Random forest models

We relied on random forest models because this machine-learning technique has been increasingly used in ecological and macro-ecology studies (Cutler et al., 2007; Kampichler et al., 2010) to assess the impact of various drivers on the extinction risks of a given group of species (Davidson et al., 2012; Di Marco et al., 2014; Di Marco et al., 2018; Buechley and Şekercioğlu, 2016; Buechley et al., 2019). In particular, the method is robust to both phylogenetic inertia and outliers, and can include both continuous and categorical variables (Murray et al., 2011; Davidson et al., 2012; Buechley et al., 2019). This technique is therefore particularly suitable for columbids given that their phylogenetic relationships are not fully resolved due to scarce sampling of taxa and limited availability of sequence data (Khan and Arif, 2013; Bruxaux et al., 2018).

We excluded extinct species and data deficient species from our analyses relying on RFs (Figure 1). We performed three different RF models to identify the factors influencing extinction risk, population trends, and scientific attention among columbids, including all traits listed and detailed in Table 1 as explanatory variables. We considered a wider range of threats than the ones considered by IUCN, thus reducing the risk of circularity when using IUCN status as a proxy of extinction risk of columbid species. All models were performed using the R software (v4.1.1, R Core Team, 2021), using RandomForest package (Liaw and Wiener, 2002). Forests consisted of 10,000, 10,000 and 1,000 classification trees for models implying respectively extinction risk, population trends and scientific attention, in order to reach the lowest value of Out Of Bag errors (OOB; i.e., the percentage of error in predicting the class of these statistical individuals across the random forest formation, see Supplementary Material 1, Method A2), which was also stable throughout the formation of the forest. To evaluate the accuracy of our classification models, we relied on the percentage of species correctly classified (i.e., 100% − OOB), Cohen's kappa statistic that tests the consistency between the actual and predicted classifications, and the sensitivity, specificity and the true skill statistic (TSS = sensitivity + specificity − 1; Allouche et al., 2006; Prasad et al., 2006; Gamer et al., 2019). For the RF addressing scientific attention (quantitative variable), we included the current IUCN category status (threatened/non-threatened) and population trends as explanatory variables. We relied on the percentage of variance explained (R^2) as accuracy metrics to assess the performance of the model. The number of variables tested at each split was determined by the program (*mtry*; root-squared of the total number of explanatory variables). We estimated the relative importance of each explanatory variables implied in RF

TABLE 1 Traits used as explanatory variables in random forest models.

Class	Variables	Description	Source
Environment	Altitude	Averaged altitude at which species occurs (x10^2 m).	BirdLife International, 2021
Environment	Dist. to continent ‡	Distance to the closest continent (km). Species being even partially on continent are set at 0. This variable was normalized using log (x+1) transformation in order to improve graph quality.	Sayre et al., 2019; BirdLife International, 2021; data.gouv.fr
Environment	Endemicity ‡	Species occurring in one country (Yes/No).	BirdLife International, 2021
Environment	Hurricane frequency ‡	Number of hurricanes ranked at least 3 in the Saffir-Simpson scale per year, since 1980. Hurricanes are known to affect avifauna (Wunderle 1995).	Knapp et al., 2010
Environment	IBA	Overlap between historical species range and Important Bird and Biodiversity Areas (Yes/No).	BirdLife International, 2021
Environment	Prop. in islands ‡	Proportion of historical species range on islands. Islands species are usually more prone to extinction (Wood et al., 2017)	Sayre et al., 2019; data.gouv.fr
Environment	Prop. in biodiv. Hotspot ‡	Proportion of historical species range overlapping with biodiversity hotspots.	Hoffman et al., 2016
Environment	Range size ‡	Historical geographic range size of species (km²). This variable was normalized by log transformation in order improve on graph quality. This variable is a strong predictor of species vulnerability (Staude et al., 2020, Newsome et al., 2020)	BirdLife International, 2021
Environment	Island endemic ‡	Restriction of historical species range to a single country consisting of one or several islands (Yes/No). Island-endemic species are usually more prone to extinction (Wood et al., 2017)	Sayre et al., 2019; BirdLife International, 2021; data.gouv.fr
Environment	Prop. in tropical ‡	Proportion of historical species range between the northern and the southern tropics.	Manually created
Behaviour and Life history	Fecundity	Average clutch size.	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Diet	Seven diet categories: granivorous, frugivorous, herbivorous (parts of plants other than seeds or fruits. e.g., buds), invertebrates eaters, meat, fungi and/or reptiles. The last three diet are very rare. For models, they were coded for each 0 (not have this diet) and 1 (having this diet).	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Diet breadth	Number of diet categories per species	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Forest dependency	Forest dependency of species. (No forest sp. (No)< Low (Lo)< Medium (Mid)< High (Hi))	BirdLife International, 2021
Behaviour and Life history	Generation length	Generation length of species from Birdlife International. The variable is known to impact extinction risk in birds (Bird et al., 2020).	BirdLife International, 2021
Behaviour and Life history	Sociality	Sociality of species. (Gregarious (Greg.)/Occasionally gregarious (Occ.)/Solitary (Sol.))	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Life stratum	Stratum in which the species live (Arboreal (Arb.)/Ground (Gr.)/Both).	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Mass	Averaged body mass of species (g). This variable was normalized using log transformation to improve graph quality.	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Migration	Migration status: Full migrant (Full.)/Vagrant (Vag.)/Sedentary (Sed.)	BirdLife International, 2021; Birds of the world; Gibbs et al., 2001

(Continued)

TABLE 1 Continued

Class	Variables	Description	Source
Behaviour and Life history	Habitat breadth	Number of different habitats used, based on Habitat level 2 from Birdlife International.	BirdLife International, 2021
Pressure	Subsistence use	Species hunted for subsistence purpose, as defined by IUCN red list (Yes/No).	BirdLife International, 2021
Pressure	Handicraft use	Whole or parts of the species used for crafting jewellery, ornament, or any items (Yes/No).	BirdLife International, 2021
Pressure	HFP ‡	Geometric mean of human footprint values estimated in 2009 (see Di Marco et al., 2018 and Venter et al., 2016 for detailed explanation).	Venter et al., 2016; Venter et al., 2018
Pressure	IAS birds	Species impacted by invasive alien bird species (Reported/Not Reported).	BirdLife International, 2021
Pressure	IAS mammals	Species impacted by invasive alien mammals species (Reported/Not Reported).	BirdLife International, 2021
Pressure	IAS reptiles	Species impacted by invasive alien reptiles species (Reported/Not Reported).	BirdLife International, 2021
Pressure	Pets use	Use of species used as pet or display (Yes/No).	BirdLife International, 2021
Pressure	Sport hunting use	Species exposed to sport hunting (Yes/No).	BirdLife International, 2021
Socio-political indicator	GSI ‡	Governance stability index. This index is the average of six indices that measures governance (voice and accountability, political stability and absence of violence, government effectiveness, regulatory quality, rule of law, and control of corruption (Baynham-Herd et al., 2018).	World Bank database
Socio-political Indicator	HDI ‡	Human Development Index. This index is based on life expectancy, years of schooling and gross national income per capita.	World Bank database
Socio-political indicator	Human density ‡	Number of humans per km^2. Averaged over estimates for 2000, 2005, 2010 and 2020.	CIESIN, 2018

‡ means that data were extracted using GIS tools.

models based on the mean decrease Gini (when the dependent variable is qualitative or classes) or increase in node purity (when the dependent variable is quantitative), as a measure of how much model accuracy decreases when removing explanatory variables. The calculation is based on the Gini/node impurity value estimated from classification trees composing the forest. Detailed explanations about random forest modelling are provided in Supplementary Material 1, Method A2.

After inspecting partial dependence plots of relationships between explanatory and dependent variables, we restricted the analysis to the eight first most important variables, as the other ones were much less meaningful and did not present enough variation (Supplementary Material 2, Figure A4–A7). In order to compare and statistically assess the relative importance of explanatory variables and partial plots, we calculated 95% confidence interval (95%CI) by performing 1,000 independent bootstraps from the original dataset (Cumming and Finch, 2005). Results of inferential statistical tests (i.e., tests of Wilcoxon, Kruskal-Wallis, Kendall's correlation or Fisher) are presented in Supplementary Material 2 (Table A1–A3), for all explanatory variables.

Although accuracy metrics were calculated for each RF model, we assessed the prediction capacity of models addressing extinction risk and evaluated overfitting issues by randomly splitting the original dataset into a training dataset (80% of the original dataset) and a dataset that was used to make predictions about extinction risk (i.e., the remaining 20% of the original dataset). Thereafter, we compared predicted results to actual ones by calculating sensitivity, specificity and TSS. This process was renewed 1,000 times in order to calculate the mean and 95% confidence interval of the three performance statistics. Thereafter, we predicted extinction risk for all columbid species by excluding one by one each species from the training dataset (i.e., all species, excepted the species tested). As we found mismatches between predicted and actual extinction risk for some species, we assessed to what extent this was related to levels of scientific attention. To that end, we considered two groups based on the median of scientific attention (i.e., one). The first group then consisted of species for which more than one published scientific article was available whereas the second one corresponded to species for which one or zero scientific article was available. We then tested for differences in the relative proportions of mismatches and correctly evaluated species between the two groups using a Chi-square test. For both analyses, significance level was set at 0.05.

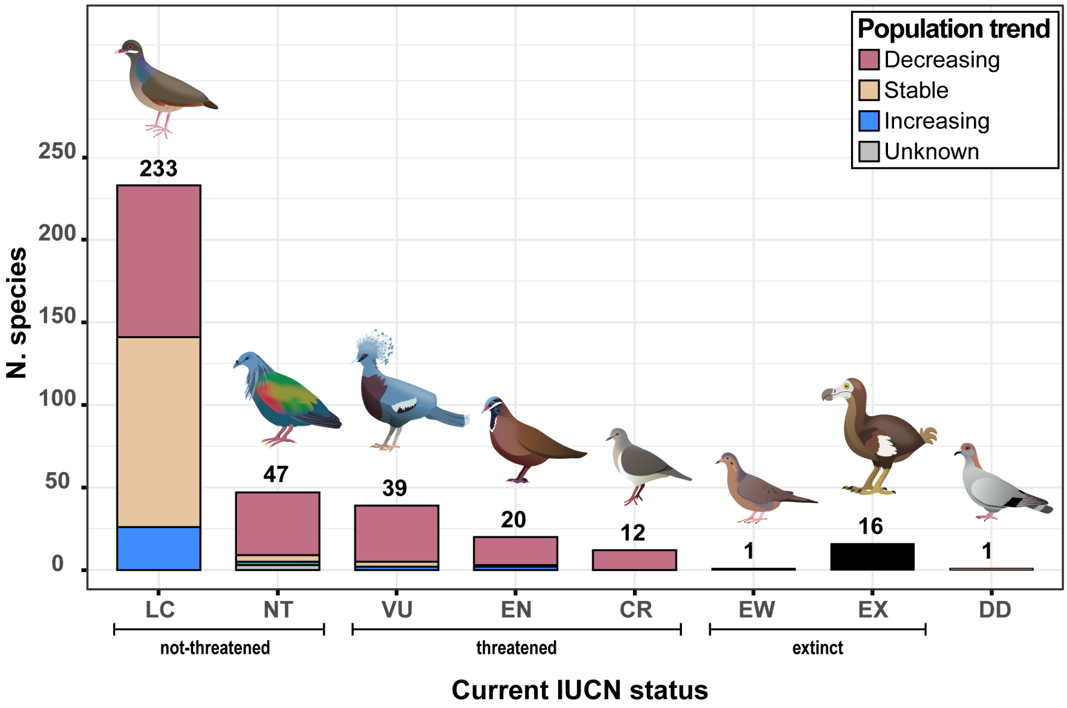

FIGURE 1
Distribution of columbid species according to their current IUCN status and their current population trend. From left to right, columbid species illustrations correspond to: Bridled Quail-Dove (*Geotrygon mystacea*), Nicobar Pigeon (*Caloenas nicobarica*), Victoria Crowned-Pigeon (*Goura victoria*), Blue-headed Quail-Dove (*Starnoenas cyanocephala*), Grenada Dove (*Leptotila wellsi*), Socorro Dove (*Zenaida graysoni*), Dodo (*Raphus cucullatus*) and Somali Pigeon (*Columba oliviae*).

3 Results

Among the 369 described columbid species, 76% are considered by IUCN as non-threatened and 19% as threatened, and 5% as extinct or extinct in the wild (Figure 1). In terms of population trends, 52% of species are declining, while 33% are stable and 9% are increasing. As expected, the relative proportions of declining, stable, and increasing species differed between threatened and non-threatened ones [threatened species: 89%, 6%, and 5%, respectively; non-threatened species: 46%, 43%, and 11%, respectively; Fisher's exact test, P< 0.0001].

3.1 Extinction risk

3.1.1 Threatened *vs*. non-threatened species

The RF model classifying species either as non-threatened or threatened correctly classified 87% of the species based on the 38 explanatory variables used (Table 1). RF model sensitivity and specificity respectively indicated that 87% of actual non-threatened species and 82% of actual threatened species were correctly identified. Cohen's kappa statistics and TSS further indicated that the classification of species significantly differed from a random classification [Cohen's kappa = 0.51, P< 0.0001; TSS = 0.70], while the OOB error was 13%. The eight most important variables influencing extinction risk were in decreasing order: species historical range size, impact of invasive alien mammals, distance to closest mainland, altitude distribution of the species, HFP, human density, proportion of species historical range in current biodiversity hotspots, and species body mass. Based on the 95% CI comparison, only historical geographic range size had a relative importance significantly higher than the other variables (Figure 2A, see Supplementary Material 2, Figure A4 for all variables importance values). Based on partial dependence plots, species with the smallest historical range size, exposed to invasive alien mammals, living the farthest to mainland and/or at the lowest altitudes were associated to a greater risk of extinction (Figure 3A). Although other variables were relatively important in the prediction of species' risk extinction based on the RF model, their variation did not seem to be directly associated to extinction risk (Figure 3A; see Supplementary Material 2, Figure A5 for all variables).

3.1.2 Population trends

The RF model correctly classified 73% of species according to population trends, with a OOB error of 27%. In addition, the percentage of true positive was of 74%, 69% and 64% for decreasing, stable and increasing species, respectively. On the other hand, the percentage of true negative was of 80%, 89% and 94% for decreasing, stable and increasing species' population trends, respectively. Although goodness-of-fit was lower than for the previous model, Cohen's kappa still indicated a species classification differing from a random classification [Cohen's kappa = 0.48, P< 0.0001]. The eight most important variables predicting population trends were in decreasing order: human density within the species historical geographic range distribution, species body mass, HFP, species historical geographic range size, species habitat breadth, GSI, species altitude distribution, and HDI (Figure 2B). Based on the comparison of 95%CI, these eight variables

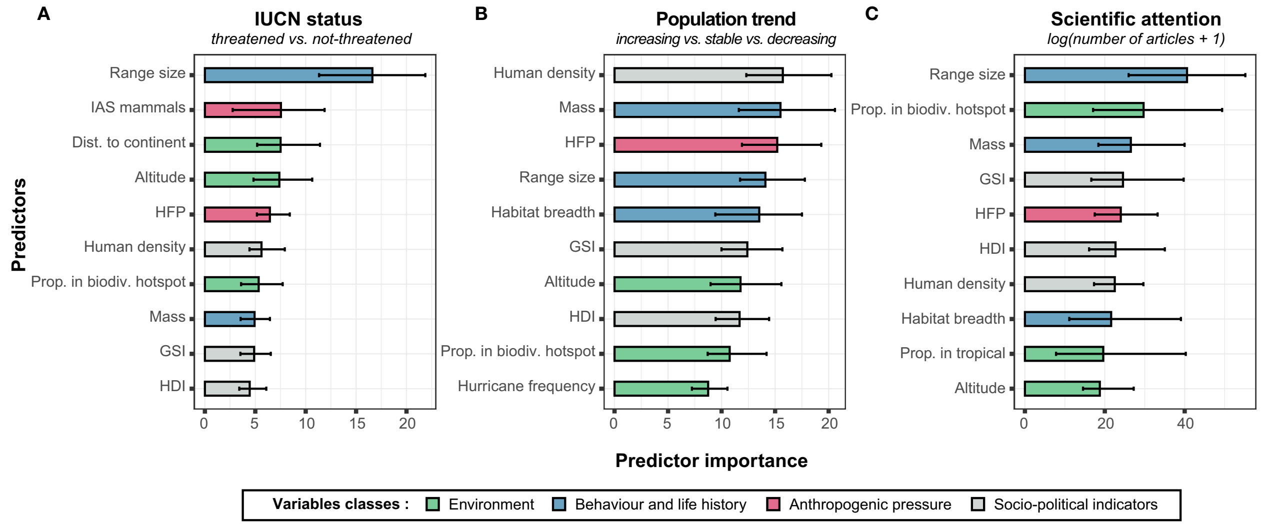

FIGURE 2
The relative importance of each explanatory variables implied in RF models with **(A)** IUCN status, **(B)** population trend and **(C)** scientific attention as explained variables. Only the ten most important variables are presented here. See Supplementary Material 2, Figure A4 for all explanatory variables.

did not seem to significantly differ in terms of importance (Figure 2B, see Supplementary Material 2, Figure A4 for all variables importance values). Based on partial dependence plots, risk of population decline was significantly lower for species with a low body weight living in areas characterized by high human density (Figure 3B). In addition, a higher risk of decline was associated with species with narrow habitat breadth and living at low altitudes (Figure 3B). Although other variables were important in predicting species' risk of decline based on the RF model, partial dependent plots suggest that they are not directly associated to it (Figure 3B; see Supplementary Material 2, Figure A6 for all variables).

3.2 Scientific attention

Our literature survey resulted in 3,537 research articles across the 369 Columbidae species, in scientific disciplines related to environment, ecology and evolution. From these articles, 405 concerned multiple species. Scientific attention (assessed from the number of published articles) differed markedly between columbid species, ranging from 0 to 1363 (median = 1, interquartile = 3). Overall, 10 species (about 3% all species) accounted for 77% of all research articles published since 1966. The most commonly studies species were the Common Wood Pigeon (*Columba palumbus*, 1363 articles), the Rock Pigeon (*Columba livia*, 1079), the Mourning Dove (*Zenaida macroura*, 309), the European Turtle-Dove (*Streptopelia turtur*, 121), the Eurasian Collared-Dove (*Streptopelia decaocto*, 117), the Common Ground Dove (*Columbina passerina*, 115), the Malagasy Turtle Dove (*Nesoenas picturatus*, 93), the Zenaida Dove (*Zenaida aurita*, 79), the White-winged Dove (*Zenaida asiatica*, 65) and the Plain-breasted Ground Dove (*Columbina minuta*, 46). Among them, only the Eurasian Turtle Dove is listed as vulnerable with a high risk of extinction, whereas the nine other species are considered of least-concern. In contrast, we did not find any article for 151 (41%) species. Overall, scientific attention was negatively associated with IUCN status [Jonckheere-Terpstra test, JT= 13864, P = 0.006].

Research laboratories in North America and Europe contributed the most to research on columbid species, accounting for, respectively, about 43% and 32% of articles published in peer-reviewed journals. Scientific attention by country was positively correlated with GSI and HDI, but negatively with HFP (Supplementary Material 2, Table S5). Based on geographic distribution of species, species inhabiting close to "hotspots" of research on columbid species were the most studied (Figure 4, 5). The geographic distribution of scientific attention was also positively correlated with GSI and HDI, and, contrary to scientific attention *per se*, to HFP (Figure 4). Accordingly, the vast majority of unstudied species were located in the southern hemisphere, while most of the 10 most studied species were totally or partially located in the northern hemisphere (Figure 5).

Based on RF models, explanatory variables accounted for 45% of the observed variation in scientific attention among columbid species. The most important variables were species historical geographic range size, proportion of species range in current biodiversity hotspots, species body mass, GSI, HFP, HDI, human density within species range, and species habitat breadth (Figure 2C). In terms of relative importance, the historical range size of species did not differ from the proportion of species range in current biodiversity hotspots, species body mass of species, GSI, and species habitat breadth, as evidenced by their 95%CI (Figure 2C). The importance of other variables was lower (Supplementary Material 2, Figure A4). Partial dependence plots show that species with important range size, high body mass, occurring in countries with highest values of GSI, and located in ecosystems highly impacted by human activities (high HFP value) have been the most studied (Figure 4). Although no clear association was observed with the proportion of species range within hotspots of biodiversity, there was a trend for species exclusively occurring in biodiversity of hotspots to be less studied than others (Figure 4). In addition, we observed a positive trend relating scientific attention to species habitat breadth (Figure 4). Although the others variables were more or less important to explain scientific attention variation based on RF model,

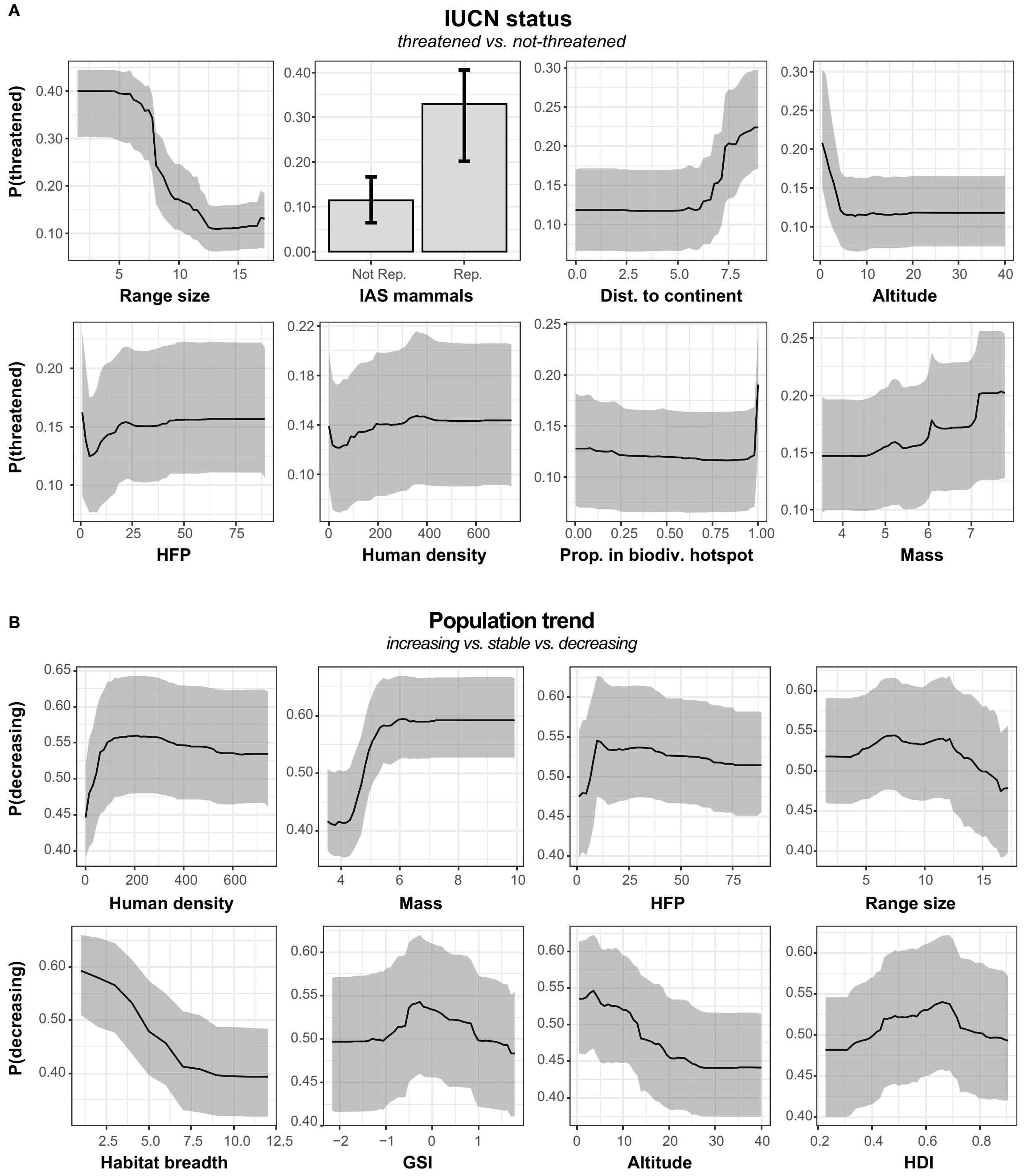

FIGURE 3
Partial dependence plots illustrating **(A)** the probability to be threatened and **(B)** the probability to have decreasing population trend in relation to the top eight predictors according to relative importance (Figures 2A, B). See Supplementary Material 2, Figure A5–A6 for partial dependence plots of all explanatory variables.

their variations were not directly associated to scientific attention (see Supplementary Material 2, Figure A7 for all variables).

3.3 Extinction risk predictions biased by scientific attention

Bootstrapped sensitivity and specificity [95% CI] of the extinction risk model respectively indicated that 78% [46%; 100%] of actual non-threatened species and 87% [78%; 95%] of actual threatened species were correctly identified when randomly using 80% of original dataset as training data, and the remaining 20% as tested data. Moreover, bootstrapped TSS [95% CI] was significantly different from zero (0.649 [0.328; 0.902]) showing that random training datasets classified species better than a random classification. Besides, these values were not significantly different from those calculated from the global model, thus suggesting an absence of overfitting.

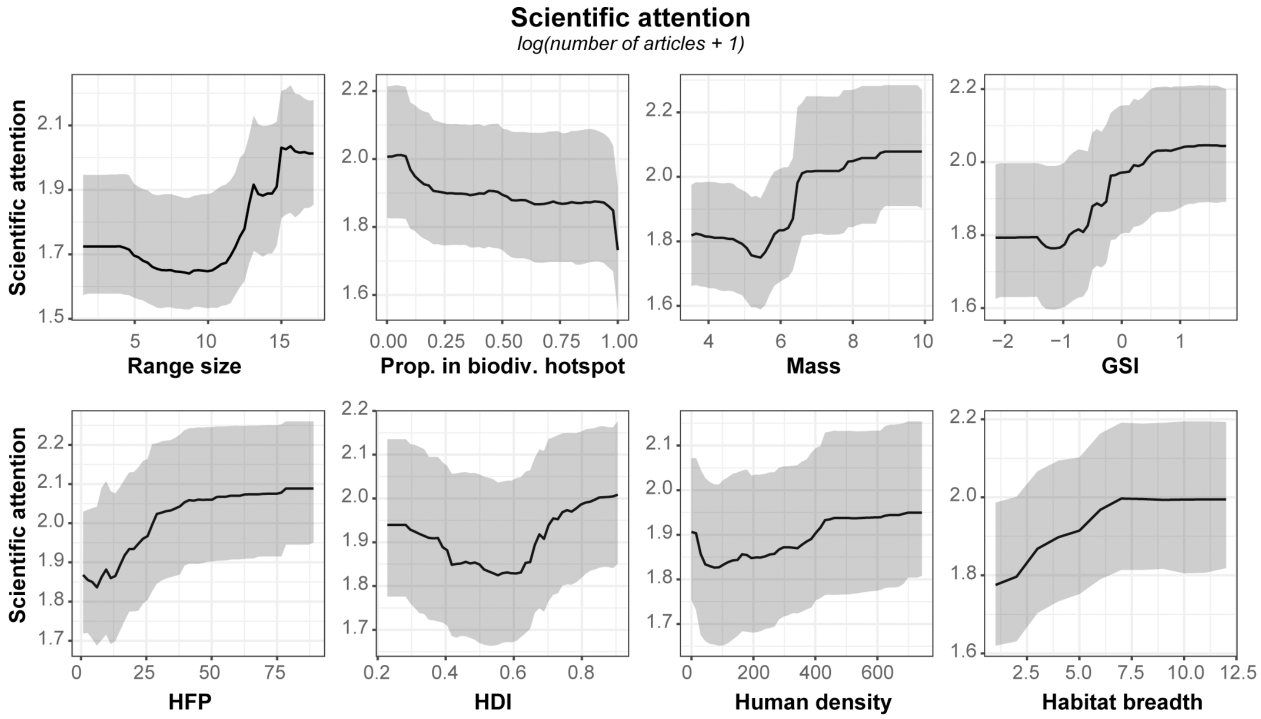

FIGURE 4
Partial dependence plots illustrating scientific attention in relation to the top eight predictors according to relative importance (Figure 2C). See Supplementary Material 2, Figure A7 for partial dependence plots of all explanatory variables.

Among the 352 extant columbid species, the prediction of extinction risk of 50 species (14%) was inconsistent with their actual status (see Supplementary Material 2, Table A5 for a detailed list). On the one hand, the model predicted a higher extinction risk than that indicated by the IUCN red list for eight of them (16%), with estimated probabilities to be classified as "threatened" by the model being above or equal to 50%. On the other hand, the model suggested to downlist most of these species (42, 84%) as "not threatened". However, their average estimated probability to be classified as "threatened" by the model was 30% ± 13% (SD), and only ten of them had an estimated probability to be classified as "threatened" inferior to 20%. Importantly, we found that mismatches predictions in term of extinction risk were significantly related to scientific attention. Species with

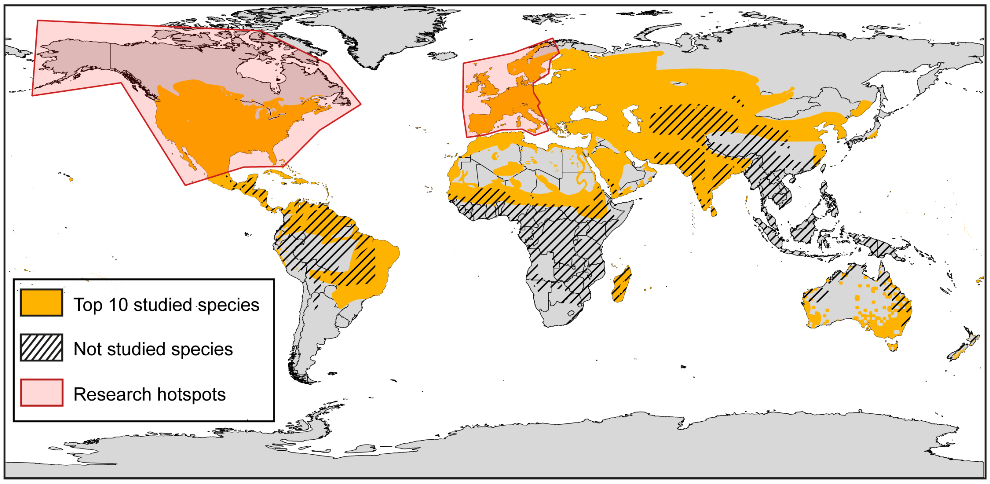

FIGURE 5
Maps illustrating the geographical distribution of the top 10 studied species and not studied species. The two most important research hotspots correspond to the regions of North America (USA + Canada) in the left, and of Western Europe in the right. They represent about 70% of the scientific production in natural sciences among the first 50 countries according to the Nature index database (https://www.nature.com/nature-index).

mismatches prediction were in fact less studied than those with predictions consistent with the IUCN red list [Chi-square test, $X^2_{(1)} = 7.336$, P = 0.007]. The only species classified as data deficient in the IUCN red list, *Columba oliviae*, was classified as "not threatened" by the model, with a probability of 79%.

4 Discussion

Since Walker (2007), the number of identified species of Columbidae has increased from 317 to 370 species. Meanwhile, the proportions of extinct (4.30% in the present study and 3.70% in Walker, 2007), threatened (19.24% and 18.61%, respectively) or non-threatened species (75.88% and 77.29%, respectively) have however remained stable. Walker (2007) described the geographic distribution of columbid species across the world according to their extinction risk and associated threats, as listed in the IUCN red list. We went further by quantitatively assessing to what extent various biological, ecological, environmental and socio-political drivers influence extinction risk and population trends of columbid species as well as interspecific variation in levels of scientific attention. In addition, we showed, for the first time, that low scientific attention can be responsible for incorrect estimation of the conservation status of columbid species.

4.1 Extinction risk

4.1.1 Ecological and biological drivers

Overall, our results tend to agree with previous findings (Walker, 2007) about the main drivers of extinction risk. However, we show that the use of both IUCN status and population trends are complementary in the identification of these drivers. Using both of them allowed us to identify several biological and ecological traits that make columbid species more prone to extinction. First, range-restricted species appeared more prone to extinction than more geographically widespread ones. Such relationship might seem obvious when using IUCN status as a proxy of extinction risk, because geographic range size is considered in its assessment (Fisher and Owens, 2004). However, geographic range size of columbid species was also positively associated with risk of population decline, thus confirming this factor as an important predictor of global extinction risk. Although the impact of geographic range size on extinction risk is complex, small range size is often associated with restricted ecological niche and small population size. Indeed, the number of habitats or resources required for survival and reproduction of individuals and, hence, population growth, often covary with geographic range size (Gaston, 2003; Peterson et al., 2011; Saupe et al., 2015). Moreover, large-range species are overall less likely to be affected by human disturbance or destruction of their natural environment, or by stochastic events, in their entire geographic range at once (Gaston, 2003; Fisher and Owens, 2004). However, some particular migrating columbid species, despite having a large range size, might be vulnerable to disturbance or damage occurring in their breeding, wintering or stop-over areas, as shown in the case of the Woodpigeon (*C. palumba*; Schumm et al., 2022; but see Bendjoudi et al., 2015) or the Turtle Dove (*S. turtur*; Eraud et al., 2013; Schumm et al., 2021). The negative relationship between extinction risk and geographic range size has been evidenced in a large range of terrestrial and marine vertebrate species (Davidson et al., 2012; Di Marco et al., 2014; Böhm et al., 2016; Buechley et al., 2019), and at different geological time scales (Harnik et al., 2012).

Second, island columbid species appeared to be more prone to extinction than continental ones, and even more so the further the distance of islands to mainland. Indeed, in addition to usually having smaller geographic range size than continental species, island-species have evolved in isolation, under particular selection pressures (e.g., relaxed predation and parasitism), making them particularly vulnerable to disturbances such as overexploitation and any kind of negative interactions with invasive species (Purvis et al., 2000a; Purvis et al., 2000b; Boyer, 2010; Loehle and Eschenbach, 2012). Introduced pathogens may also have a significant negative impact on the persistence of isolated populations. For instance, a pathogenic strain of *Trichomonas gallinae*, which might have been introduced in Mauritius Island, increased adult and nestling mortality in the endangered Pink Pigeon, *Neosoenas mayeri* (Swinnerton et al., 2005; Bunbury et al., 2007; Bunbury et al., 2008). In mammals and birds, 95% of known extinctions concerned island-species (Loehle and Eschenbach, 2012). However, smaller geographic range size of most insular species might be the most important variable in explaining species extinction risk (Manne et al., 1999). Among columbid species, all known extinct species inhabited islands, excepted for the Passenger Pigeon (*Ectopistes migratorius*), suggesting that being an island-species is at least as much important as geographic range size, especially when adding other sources of extinction such as overexploitation, invasive species or climate change (Courchamp et al., 2003; Courchamp et al., 2014; Wood et al., 2017). For instance, the two largest known and now extinct columbid species, the iconic Dodo, *Raphus cucullatus*, and the Rodrigues Solitaire, *Pezophaps solitaria*, were both endemic to Mauritius islands and flightless. Their extinction was probably due to a combination of factors, including large body size, island endemism, low population growth, small population size and small geographic range size, making them particularly vulnerable to habitat destruction, hunting and invasive species (Duncan et al., 2002; Fisher and Owens, 2004; Hume, 2006; Hilbers et al., 2016). Our results indeed suggest that the extinction risk of columbid species increases with their body mass, as shown in diverse taxa (Gaston and Blackburn, 1995; Davidson et al., 2009; Fritz et al., 2009; Böhm et al., 2016). The influence of body size could actually be multifactorial, and be exacerbated by other external factors like overexploitation. Indeed, larger species are often preferred as game species (Duncan et al., 2002; Whytock et al., 2016; Ripple et al., 2017).

Although hunting has been recognized among the most important threats within Columbidae, concerning 77% of threatened species (Walker, 2007), and that inferential statistics performed in this study (see Supplementary Material 2, Table A1–A2) showed that threatened species are significantly more exposed to it, our models did not identify hunting-related drivers (i.e., subsistence use and sport hunting) as important variables explaining extinction risk. This does not mean that the impact of hunting exposure is null, but that other variables provide a better discriminant classification into RF models to evaluate extinction risk of columbids. It is obvious that hunting has a direct influence on the mortality rate of harvested populations, and, hence, can be a contributing driver to extinction risk for some species (e.g., the European Turtle Dove, *Streptopelia turtur*, Lormée et al., 2020), especially when it is not regulated or not performed in a sustainable way. However, the assessment of extinction risk requires a more comprehensive approach, considering various drivers and threats, as discussed in management recommendations for the European Turtle Dove (Bacon et al., 2023). The global influence of hunting might thus be lower than that of other threats, such as habitat loss and invasive species. However, its impact on game populations might be exacerbated when combined with such threats (Romero-Muñoz et al., 2019; Romero-Muñoz et al., 2020; Bogoni et al., 2022). For instance, the extinction of the iconic Passenger Pigeon was caused by both unregulated commercial hunting and significant destruction of its breeding habitat (i.e., a decrease estimated about 53%; Stanton, 2014). Furthermore, a more precise metrics of hunting pressure would probably be more informative than mere exposure to hunting (Bellard et al., 2022) and could have enhanced the performance of our RF models. Unfortunately, such information is unavailable for a large majority of game columbids.

Habitat breadth also appeared to influence extinction risk, confirming a general trend (Norris and Harper, 2004; Devictor et al., 2008; Clavel et al., 2011; Callaghan et al., 2019). Although ecological specialization does not always limit the capacity of species to persist (Benito et al., 2020), it might be evolutionary disadvantageous in environments exposed to changes and perturbations (Davies et al., 2004; Colles et al., 2009; Clavel et al., 2011; Ducatez et al., 2014; Morelli et al., 2020). Indeed, specialist species often tend to be associated with small population size, restricted geographic range size and limited use of resources and habitats, what may make them particularly vulnerable when exposed to environmental changes and disturbances (McKinney, 1997; Davies et al., 2004; Colles et al., 2009).

4.1.2 Anthropogenic drivers

Not surprisingly, our analysis points to alien invasive species as an important factor affecting the risk of extinction of columbid species (Walker, 2007). Exotic species are indeed a major threat to biodiversity, as a result of predation, parasitism, competition, hybridization with native species and the disturbance of native ecosystems (Mack et al., 2000; Sax and Gaines, 2008; Walsh et al., 2012). Invasive mammals, especially rodents (e.g., rats *Rattus* sp.) and cats (*Felis catus*), are the most damaging group of alien species across all ecosystems. Both are responsible of more than 30% of all known contemporary extinctions, especially on islands (Doherty et al., 2016). Invasive species can predate native columbid species (Rodriguez-Estrella et al., 1991; Tidemann et al., 1994; Zarzoso-Lacoste et al., 2016; Lamelas-López et al., 2020), compete with them for resources (James and Clout, 1996; Bond et al., 2019), or transmit pathogens (Stimmelmayr et al., 2012). Based on IUCN data, 9% of all columbid species have been reported to be exposed to invasive rats, 8% to cats, and 12% to other mammals (IUCN, 2021). Among non-threatened species, 3% of species have been reported to be exposed to invasive mammals, compared to 35% for threatened species and 77% for extinct species. However, the precise impact of invasive mammal species on the demography of columbid species of patrimonial interest in the wild remains to be quantitatively assessed in order to assess to what extent it compares in importance with hunting pressure or habitat loss and thus provide a more comprehensive and integrative approach to the management of species/populations.

Although global warming is supposed to increase extinction risk among species living at high altitude (Williams et al., 2003; Shoo et al., 2005; Sekercioglu et al., 2008; Bässler et al., 2010; La Sorte and Jetz, 2010), we found no evidence for a positive relationship between extinction risk and elevation in columbids. The consequences of global warming on extinction risk at higher elevation might not be felt yet (Bellard et al., 2012) in columbid species, or might have been hidden in our analysis by variation in habitat breadth and more intense human activities at lower elevations. Indeed, landscape heterogeneity tends to decrease with increased elevation, and species found at elevation tend to have a higher degree of ecological specialization than those found at lower elevation (Reif et al., 2013; Rivas-Salvador et al., 2019). Lower elevations are also associated with higher anthropogenic transformation, inducing various negative effects on local biodiversity (Ellis et al., 2010; Reif et al., 2013; White and Bennett, 2015; Smith et al., 2019). Further attention should then be given to the influence of elevation on the demographic trends of columbid species in relation to climate change and habitat modification.

Several other drivers of anthropogenic origin appeared to contribute, directly or indirectly, to increase the extinction risk of columbid species, such as low levels of governmental stability and poor socioeconomics and/or the loss and disturbance of natural habitats through the development of HFP. HFP provides an index of human conversion of natural terrestrial ecosystems based on the measure of eight different anthropogenic pressures related to urbanization, agriculture and human density (Venter et al., 2016), and can therefore be regarded as a proxy of habitat degradation or loss. Yearly variations in HFP have been found to be a good predictor of extinction risk in terrestrial mammals (Di Marco et al., 2018). Although some columbid species flourish in landscapes modified by humans, such as the widespread Feral Pigeon, *Columba livia domestica* (Carlen et al., 2021), the Zenaida Dove, *Zenaida aurita* (Wolff et al., 2018), or the invasive Eurasian Collared-Dove, *Streptopelia decaocto* (Luna et al., 2018), most species rely on their natural habitats to persist. For instance, the occupancy of the Kereru, *Hemiphaga novaeseelandiae*, an endemic New Zealand Pigeon, has been affected by habitat loss resulting from European settlement in New Zealand (Carpenter et al., 2021). Following Walker (2007), the present study confirms that the loss of natural habitat is the greatest cause of extinction and populations decline in columbid species.

Governmental and socioeconomic factors were also found to affect the extinction risk of columbid species, with species inhabiting in developing countries being more exposed to extinction risk. Public policies can have negative or positive influences on biodiversity, through supporting or not reliable environmental and conservation projects and by protecting or not most vulnerable species and/or sensitive ecosystems (Chapron, 2014; Ripple et al., 2016). For instance, the Pink Pigeon, *Nesoenas mayeri*, have been downlisted twice, in the IUCN red list, from critically-endangered to vulnerable thanks to conservation projects lead by conservationists, private foundations and the Mauritian government (Tatayah, 2019). Globally, the socioeconomic level of countries tends to influence positively the persistence of species (Forester and Machlist, 1996; Dietz and Adger, 2003). For instance, Bösch (2021) showed that the level and speed of countries' economic-institutional development tend to be negatively associated with illegal logging, and hence, with habitat loss and biodiversity decline. The same is true for wildlife trafficking and hunting pressure, especially in developing countries where wildlife can be the sole source of proteins for isolated and/or low-income communities (Robinson and Bennett, 2002; Fa et al., 2003; Fa et al., 2009; Borgerson et al., 2016; Lescuyer and Nasi, 2016). Legal and illegal hunting can be practiced to obtain food or increased social status, or as a recreational or traditional activity (Phelps et al., 2016; Stirnemann et al., 2018). Indeed, wildlife meat consumption is not always associated with poverty and can also be a sign of wealth (Fa et al., 2009). This is for instance the case in the Pacific islands where poor people hunt both the Pacific Pigeon, *Ducula pacifica*, and the Tooth-billed Pigeon, *Didunculus strigiristris*, to sell their meat to high-income populations (Phelps et al., 2016; Stirnemann et al., 2018).

4.2 Scientific attention

In strong contrast with the ubiquity of the family Columbidae throughout the world, the order Columbiformes is among the least studied orders in the Aves class (8th/25, Ducatez and Lefebvre, 2014). The same trend has been observed, at a lower geographical scale, in the Caribbean region (Devenish-Nelson et al., 2019). One reason for the low attention given to columbids could be that this family does not include any charismatic species (Seddon et al., 2005; Devenish-Nelson et al., 2019), excepted for the iconic Dodo and Passenger Pigeon that became textbook cases due to their extinction history (Kyne and Adams, 2017).

Scientific attention on columbid species appeared to be geographically biased and independent of species extinction risk, as shown by the negative association between scientific attention, the proportion of species in biodiversity hotspots and the influence of both HDI and GSI (Livingston et al., 2016; Tydecks et al., 2018; Melles et al., 2019). In addition, we found that island-endemic columbid species were on average less studied than continental species, and even more so the farther they are from mainland (see also Brooks et al., 2008). Contrary to Ducatez and Lefebvre (2014), we did not find any association between scientific attention and clutch size or generation time, probably due to low variability in these two variables among columbids.

Most of the research on columbid species is actually done by North-American and European researchers working on local species, accounting, respectively, for about 43% and 32% of all articles published in peer-reviewed journals, whereas species living between Fiji and Indonesia, the most important hotspot for threatened columbid species and diversity (Walker, 2007), are among the least studied ones. The same geographical bias has been found in several studies focusing on diverse taxa (Ducatez and Lefebvre, 2014; Tydecks et al., 2018; Melles et al., 2019). It can be partly explained by logistic constraints, local poverty, political instability, geographic isolation and lack of local expertise in developing countries (Clark, 1985; de Lima et al., 2011; Amano and Sutherland, 2013; Wilson et al., 2016; Reboredo Segovia et al., 2020; Vallès et al., 2021).

Widespread columbids, in terms of geographic distribution or in terms of number of different habitats used, and relatively large-bodied species (>100g according to Figure 4) seemed more studied than others, as highlighted by Ducatez and Lefebvre (2014), who focused their research on bird Orders. More widespread species are presumably more accessible and have thus more chance to be studied than less widespread ones (Morales and Traba, 2016; Yarwood et al., 2019), while large species are usually easier to locate and observe than more discrete and smaller species (Ripple et al., 2017; Yarwood et al., 2019). Furthermore, we found that scientific attention on columbid species was positively associated with human density and human footprint, suggesting that columbid species inhabiting areas with high human density and highly urbanized were preferentially studied. As explained by Ibáñez-Álamo et al. (2017), species living close to humans, such as feral pigeons (e.g., Perez-Sancho et al., 2020), may receive more attention because of economic and public health issues (Lindahl and Magnusson, 2020) and/or because they are easier to study. Similarly, some applied research has been conducted on columbid species living close to humans in relation to negative impacts on crops (e.g, Murton and Jones, 1973; van Niekerk and van Ginkel, 2009; Firake et al., 2016; Verga et al., 2021). However, columbid species causing damages on crops may also experience higher extinction risk due retaliatory actions, including hunting and poisoning, by farmers (Marrero et al., 2004; Cuesta Hermira and Michalski, 2022).

5 Conclusion and perspectives

Our results quantitatively confirmed earlier findings on the main factors influencing extinction risk and population decline in columbids (Walker, 2007) and revealed large disparity in scientific attention given to columbid species, with the most threatened ones being the least studied. In this respect, species for which predicted extinction risk status were inconsistent with actual status were also the least studied. We therefore recommend to pay more attention to these species, and more generally to specialist species, restricted-range species, particularly insular ones, and/or large species, in relation to habitat disturbance and loss, in order to better estimate direct and specific extinction risk. In addition, investigations on urban populations of columbid species may help understanding interspecific variation in adaptive potential in relation to urbanization and global change.

Secondly, we strongly recommend to investigate the relative importance of sources of mortality of pigeons and doves in the wild in order to gain a more complete picture of the threats weighing on them. In this respect, it would be of interest to assess the relative importance of legal and illegal hunting compared to that of predation by exotic invasive predators in the decline of species. Columbids are indeed particularly appreciated by hunters, but are also exposed to various introduced potential predators in various regions. Although the impact of invasive mammal predators is widely acknowledged as an important threat to native wildlife, precise quantitative assessment is often lacking, particularly for columbid species. To that end, cooperation among hunters, scientists, wildlife officers and agencies should be encouraged, particularly where hunting traditions are an important part of local culture. Although difficult to implement, the regulation of invasive predators or their total eradication may have immediate positive impacts on native populations and ecosystems (Le Corre et al., 2015, Miller-ter Kuile et al., 2020).

Based on the influence of socioeconomic factors revealed here, we also recommend to develop coordinated efforts to better inform governments, public agencies and the general public of the key ecological role played by columbids and of the importance of conserving populations and associated habitats. In that respect, both extinct and extant columbid species could be used more widely in education programs about the erosion of biodiversity. Finally, fair transnational cooperation and capacity building in conservation-oriented research on columbids should be encouraged, especially between small island developing states and developed countries.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: caribaea.org.

Author contributions

CC: Conceptualization, methodology, formal analysis, data collection, data curation, writing – original draft, visualization. AJ-P: Data collection. EB: Conceptualization, supervision, resources, project administration. FC: Conceptualization, validation, writing – original draft, supervision, project administration. 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.2023.1141072/full#supplementary-material

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Arthropod communities of rice agroecosystems can be shaped both by local agricultural practices and the surrounding landscape

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Both intensive farming of paddy field crops and conventional farm management techniques have been a major cause of environmental issues in recent years. A more ecosystem-based, sustainable agricultural methodology should be utilized to help solve this dilemma. However, the joint effects of landscape and farming on arthropod communities in paddy fields are unexplored. In eco-friendly paddy fields, we postulate the arthropod diversity to be higher in fields that use ecosystem-based methods. In this study, we collected arthropods monthly using a blower-vac during the first rice crop of 2019 in Taiwan. A total of 53,522 individuals of 14 orders, 96 families, and 445 morphospecies were collected. All arthropods were identified into four functional groups. The result showed that insect communities are different between sustainable and conventional fields. Results showed that sustainable fields had a higher abundance of arthropod fauna than conventional fields. It was also apparent that the arthropod community changed along with the developmental growth of rice and in different areas. Three functional groups, *viz.,* herbivores, parasitoids, and detritivores, present the best model when the farming type was assigned as the fixed effect, while the predator reveal the best model when the farming type, landscape, and their interaction were assigned as the fixed effects. The arthropod communities have also been affected by the surrounding landscape. This study reveals that both agricultural management and landscape can have a joint effect on arthropod communities in paddy fields.

KEYWORDS

paddy field, sustainable farming, conventional farming, diversity, functional group

1 Introduction

Sustainable agriculture is a relatively new farming idea based on an ecological concept that embraces the interactions of organisms to achieve a balance and maintain the productivity of a given ecosystem. In contrast, in conventional agriculture, pesticides have been used intensively to control pests and diseases that maintain the crop yield loss and product quality (Aktar et al., 2009; Damalas, 2009). Although the usage of conventional agricultural methods can control the pest population, non-target organisms and their associated agroecosystem environments are highly threatened (Gibbs et al., 2009; Stanley, 2016). For example, the decline of arthropod predator diversity occurs (Frampton and Çilgi, 1994; Marie et al., 2018; Graf et al., 2019). Therefore, outcomes of sustainable agriculture are closely linked to the ecological environment and have resulted in several interactions being developed, such as eco-agriculture (McNeely and Scherr, 2003), natural farming (Fukuoka, 2010), organic agriculture (Geier, 2007), environmentally friendly farming (Novelli, 2018), and low-input agriculture (Daberkow and Reichelderfer, 1988). The combination of ecology and new technology can decrease the environmental costs of conventional agriculture. It is believed that the long-term application of such methods can improve the quality of resources and help preserve the ecological environment (Harwood, 1990).

The surrounding landscape of agroecosystems is also one of the important factors affecting the diversity of agroecosystem arthropods (Hendrickx et al., 2007; Mitchell et al., 2014). The whole farmland area may be separated by roads and low-density buildings. It is block-fragmented and may be surrounded by natural or semi-natural habitats such as vegetable gardens, orchards, woodlands, mountains, wastelands, streams, and artificial irrigation ditches (Verhagen et al., 2016; Haan et al., 2019). Baba and Tanaka (2016) found that ditches around fields can serve as non-rice cropping periods and overwintering habitats for Tetragnathidae spiders. Similarly, the combination of paddy fields and surrounding forests can increase the richness and abundance of grassland-dwelling spiders (Miyashita et al., 2012). Delettre and Morvan (2000) suggested that the distance from natural waterbodies affects the dispersal of Chironomidae species in agricultural areas. As the aforementioned studies suggest, different habitats around a farmland affect the make-up of the farmland's arthropod diversity and preserve the habitats for natural enemies (Rusch et al., 2010; Holland et al., 2016). Diverse habitats surrounding the farmland also help maintain the biodiversity so that agroecosystems can maintain good ecosystem services for both humans and other organisms (Landis, 2017).

Arthropods play an important role in the human economy and ecological niches of the agroecosystem (Chakravarthy and Sridhara, 2016). They are not only preyed on by high trophic-level consumers, such as birds, frogs, and reptiles but also connect and interact with other arthropods in the food web of agroecosystems. Rice (Gramineae: *Oryza sativa* L.) is an important food crop in Asia and elsewhere. The production of approximately 770 million tons per year makes rice one of the most important agricultural products produced in the world (FAO, 2017). A paddy field is both a semi-humid and semi-arid habitat that consists of a unique ecosystem that combines the properties of both wetland and dryland areas that are common in the agricultural landscape of Asia. Paddy fields are flooded in the growing stage and become dry land before the harvest season; therefore, paddy fields are also a part of the wetland (Hook, 1993; Watanabe, 2018), attracting habitation of both aquatic and terrestrial arthropods. As Bambaradeniya and Amerasinghe (2004) discussed, in paddy field agroecosystems, the highest diversity of invertebrates is arthropods, most of which are insects. Arthropod communities develop, and their success coincides with rice planting stages. Arthropods in paddy field agroecosystems are highly diverse, susceptible to paddy field conditions, and can be regarded as indicators to help understand how paddy field agroecosystem management impacts organisms (Ueno, 2012; Morrison et al., 2018).

Most of the studies regarding agricultural management and agricultural landscape effects on arthropods focus on wheat fields in temperate biomes (Moreby et al., 1994; Clough et al., 2007; Diekötter et al., 2010; Tuck et al., 2014). Taiwan is an island located at the border of tropical and subtropical climate zones. We believe that our work is the first to assess the joint effects of farming and landscape on arthropod communities in paddy fields. Taiwan is narrow in area but densely populated; hence, the total potential area for cultivation is also limited. Small and quality agricultural areas are well-developed in Taiwan, and the arthropod community of paddy fields here is different compared to those of temperate and tropical zones. Therefore, we aim to examine and compare the effects of agricultural management and landscape factors on total and dominant arthropod abundance and diversity in a subtropical zone (i.e., northeastern Taiwan). This study examines the advantages and disadvantages of paddy field management systems that are currently in practice. It also compares the relationship between various arthropod communities and the landscape surrounding these management systems. This will help establish basic information that can serve as a reference for future evaluation of agricultural management strategies.

2 Materials and methods

2.1 Arthropod sampling

We selected four sampling areas, each more than 1 km in the Lanyang Plains of Taiwan (Figure 1). Each sampling area contained two paddy fields that were used for conventional agriculture (CA) and sustainable agriculture (SA), respectively (Table 1). The distance between these two fields was more than 100 m for decreasing the effect of the farming type. The major distinction between CA and SA is that CA uses chemical pesticides and fertilizers, and SA uses non-chemical materials. The four sampling areas were located in Jiaoxi (Jx), Zhuangwei (Zw), Luodong (Ld), and Sanxing (Sx). The farming information is shown in Table 1. Arthropods were collected monthly during the first crop season, i.e., from March to June 2019. A customized blower-vac (Arida and Heong, 1992; Buffington and Redak, 1998) was used for sampling arthropods on four randomly selected plots on each field (2.5 * 2.5 square meters). Arthropods were collected from the aboveground part of rice plants in each field. Each of the sampling plots was sampled for 90 s. The samplings were preserved in 34*45-cm zipper bags, brought back to the laboratory, and preserved in 70% ethanol for further sorting and identification. All specimens were identified to at least family level and categorized as morphospecies given a serial number, following the abbreviation of order, such as Hem-03 and Dip-08. Additionally, arthropods were grouped into functional guilds, herbivores, predators, parasitoids, and detritivores, for further analysis (Dominik et al., 2017). Supplementary data to this article can be found online at https://doi.org/10.13140/RG.2.2.10367.18082.

2.2 Environmental data

For the environmental characteristics of each sampling area, we determined the spot directly between the sustainable and conventional sample areas and measured a 1-km radius from that point. Then, we measured the field size and surrounding

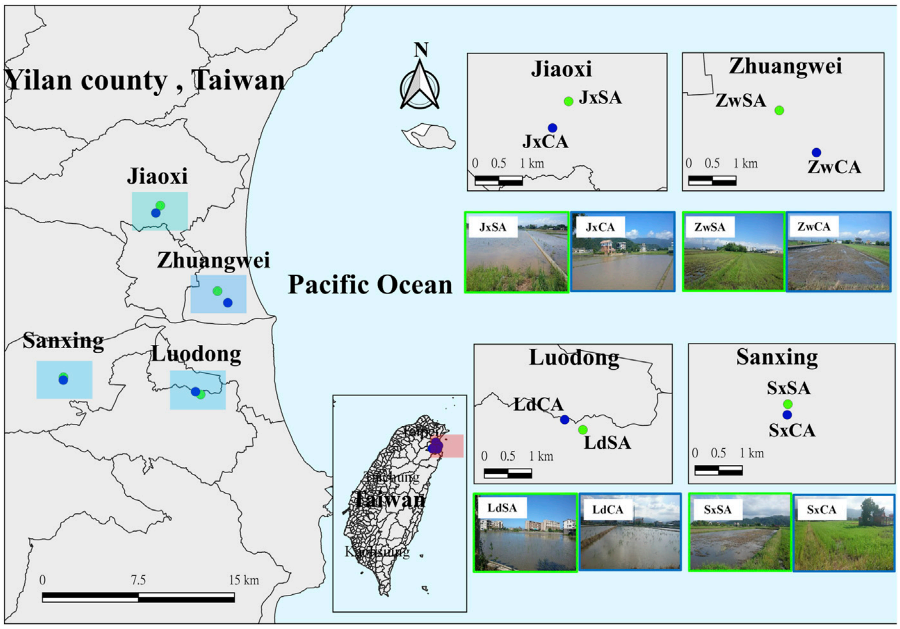

FIGURE 1
Location of the sample sites in four sampling areas in northeastern Taiwan. Green and dark blue points stand for sustainable and conventional farming fields, respectively. Jx, Jiaoxi; Zw, Zhuangwei; Ld, Luodong; Sx, Sanxing. SA, sustainable agriculture; CA, conventional agriculture.

TABLE 1 Information on the sampling sites in four sample areas in the northeastern area.

Sampling area	Location		Hectares (ha)	Rice variety	Pest control material	Fertilizer
JxSA	24°47′44.0″ N	121°45′29.0″ E	0.27	Taiken no. 8	Tea seed meal	Organic fertilizer and rice bran
JxCA	24°47′25.2″ N	121°45′17.6″ E	0.26	Taiken no. 11	Polyoxorim and isoprothiolane	Nitrogen, phosphoric oxide, and potassium oxide
ZwSA	24°44′08.0″ N	121°47′53.4″ E	0.24	Taichung Sen no. 10	Tea seed meal	Organic fertilizer
ZwCA	24°43′38.5″ N	121°48′19.5″ E	0.25	Tainan no. 11	Polyoxorim and isoprothiolane	Nitrogen, phosphoric oxide, potassium oxide, and magnesium oxide
LdSA	24°39′46.7″ N	121°47′10.9″ E	0.44	Kaohsiung no. 145	None	Organic fertilizer
LdCA	24°39′54.0″ N	121°46′57.9″ E	0.32	Taiken glutinous no. 3	Polyoxorim and isoprothiolane	Nitrogen, phosphoric oxide, and potassium oxide
SxSA	24°40′30.5″ N	121°41′24.3″ E	0.24	Tainung no. 71	Tea seed meal	Organic fertilizer
SxCA	24°40′23.2″ N	121°41′23.9″ E	0.30	Taiken no. 8	Polyoxorim and isoprothiolane	Nitrogen, phosphoric oxide, and potassium oxide

Jx, Jiaoxi; Zw, Zhuangwei; Ld, Luodong; Sx, Sanxing; SA, sustainable agriculture; CA, conventional agriculture.

landscape coverage using Google Earth Pro and ImageJ (v1.52r) software. We identified various landscape coverage, such as farmland, forest, ditch, cement (cement building and road), and stream. These ratios of coverage were presented by principal component analysis (PCA) to reveal the landscape characteristics of each sampling site (Figure 2). The Jx area possesses relatively more forests. Sx and Zw areas were occupied by paddy farms and some streams, while the Ld area has a large portion of buildings and some artificial ditches. Four sampling areas show different surrounding landscapes. In addition, the rice field size hectare, rice plant average interval, and width were measured.

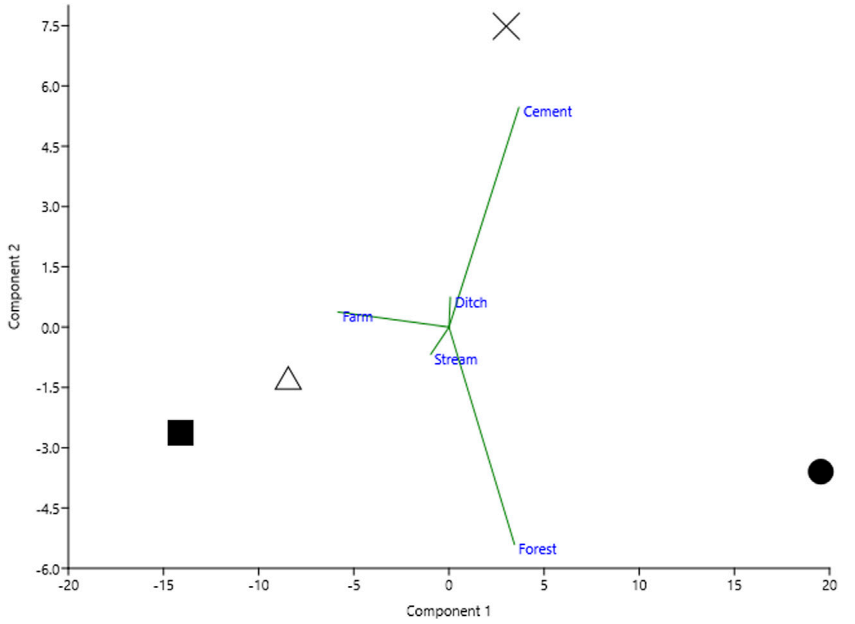

FIGURE 2
Four sampling sites characterized by five environmental data by principal component analysis. Four sampling areas are displayed by shape: circle, Jiaoxi (Jx); square, Zhuangwei (Zw); cross, Luodong (Ld); triangle, Sanxing (Sx).

2.3 Statistical analysis

We characterized the arthropod community structure by calculating the abundance, species richness, Shannon's diversity index, Simpson's diversity index, Pielou's evenness index, and Margalef's richness index for each field using Past 3.14 software (Hammer et al., 2001). To determine whether the arthropod communities were affected by the season, farming type, and landscape, we used permutational analysis of variance (PERMANOVA) performed by the package 'vegan' within the R statistical framework (version 4.0.0). The abundance of all arthropods was log-transformed prior to analyses to meet the assumptions of normality (Pinheiro et al., 2014). To measure the differences in the species structure among study sites, we performed non-metric multidimensional scaling (NMDS) ordinations after the computation of a Bray–Curtis dissimilarity matrix based on arthropod abundances.

To determine whether the abundance of each ecological group was affected by the farming type or landscape, we used generalized linear mixed models (GLMMs) performed by the lme4 package within the R statistical framework (version 4.0.0). The farming type, landscape, farming type + landscape, and farming type*landscape were assigned as fixed effects sequentially. The model with the lowest Akaike's information criterion (AIC) is regarded as the best. In the GLMM, the farming system is a binary variable (either a conventional or sustainable system) in the model, while the landscape was represented by four sampling sites (Jx, Zw, Ld, and Sx, Figure 2). Other field characteristics, including the rice field size hectare, rice plant average interval, and width, were assigned as random effects. A stepwise regression procedure was used together with testing all variable combinations to determine the best-fitting model based on the lowest AICc score. The procedure was repeated separately for each response variable and spatial scale. Each response variable has a Poisson distribution in the model.

3 Results

In total, 53,522 individuals of 14 orders, 96 families, and 445 morphospecies were collected overall for sampling during the study period (Figure 3). The arthropod composition varied among different sampling sites (Figure 3). The arthropod communities located in Jx were characterized by Thysanoptera (35%) and Hemiptera (18%) in SA farming, while Diptera (43%) was the most abundant taxa in CA farming. In Zw, Hemiptera (54%) was the most dominant taxa in SA farming, while Diptera (38%) and Acariformes (26%) were more abundant in CA farming. In Ld, Diptera was seen in SA farming and CA farming (31% and 48%, respectively). Regarding Sx, both Thysanoptera and Hemiptera were the most dominant taxa in SA farming (34% and 39%, respectively) and CA farming (39% and 32%, respectively) (Figure 3). Dominant taxa (90% of all arthropods) presented by NMDS showed that each type of paddy field was separated by different dominant arthropods (Figure 4). Overall, more hemipterans (specifically Delphacidae and Cicadellidae) and thysanopterans (almost Thripidae) inhabit the SA farm, while more dipterans (specifically Chironomidae) occurred in the CA farm.

According to the PERMANOVA analysis, the arthropod abundance was significantly different among months (F = 6.55, $p < 0.001$), the farming type (F = 2.29, $p < 0.05$), and area (F = 1.95, $p < 0.005$). The arthropod composition varied along with the growing stages of the paddy field, from the seedling (March) to the mature stages (June). Diptera (specifically Chironomidae) was dominant in the seedling stage, while Hemiptera and Thysanoptera

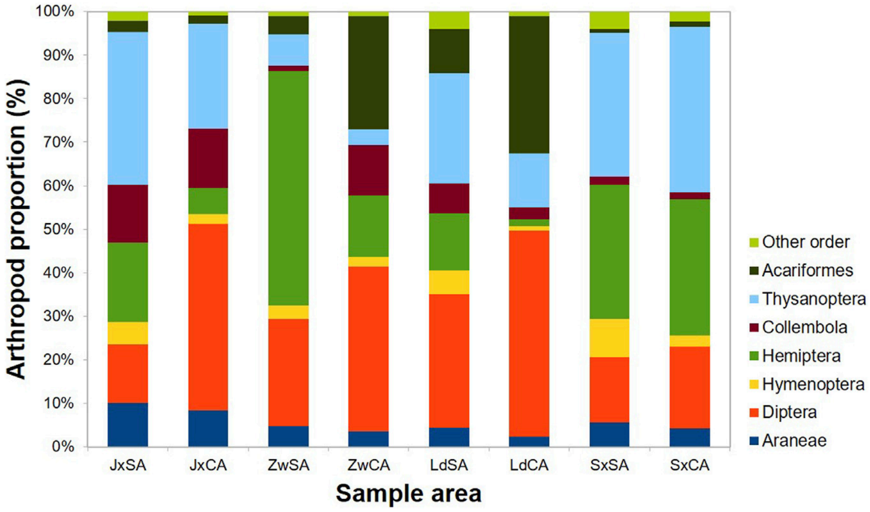

FIGURE 3
Fraction of abundance of order-level terrestrial arthropods in four sample areas in northeastern Taiwan. SA field, sustainable agricultural field; CA field, conventional agricultural field; Jx, Jiaoxi; Zw, Zhuangwei; Ld, Luodong; Sx, Sanxing.

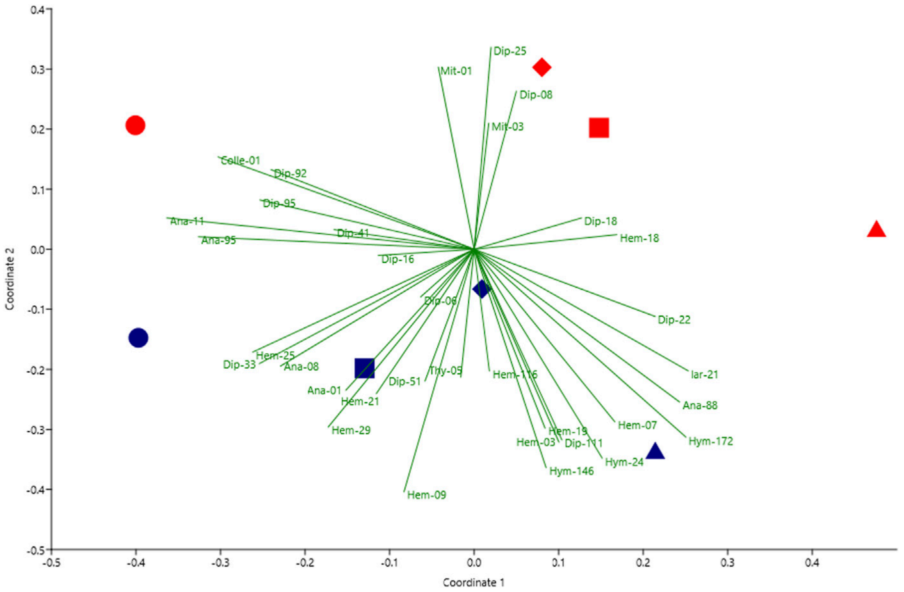

FIGURE 4
Non-metric multidimensional scaling (NMDS) analysis of the Bray−Curtis dissimilarity matrix represented by 34 dominant taxa (90% of all arthropods). Each point represents each paddy field. Sampling areas are displayed by shape: circle, Jiaoxi (Jx); square, Zhuangwei (Zw); diamond, Luodong (Ld); triangle, Sanxing (Sx). The farming type is marked by color: blue, sustainable agriculture (SA); red, conventional agriculture (CA) (stress = 0.091).

(major herbivores) were dominant in the latter stages. The arthropod community was more abundant under SA farming compared to CA farming (Table 2). Generally, the number of arthropod families, morphospecies, and species abundance in SA farming was higher than that in CA farming, except for the Ld sampling area (Table 2). Shannon's Index, Simpson's Index, Pielous's Index, and Margelef's Index indicate that the diversity was higher in SA farming than those in CA farming. LdSA has the highest diversity index, while LdCA has lowest (Table 2).

Regarding the ecological guilds, herbivores accounted for 53.2% of the total arthropods collected and were dominated by white-backed planthoppers (*Sogatella furcifera*), leafhoppers (*Macrosteles striifrons*), and the rice thrips (*Stenchaetothrips biformis*). Predators contributed 7.5% of the total abundance and were mostly

TABLE 2 Biodiversity indicator results of sample sites in four sample areas in northeastern Taiwan (SA, sustainable agriculture; CA, conventional agriculture).

Sample area	Jiaoxi		Zhuangwei		Luodong		Sanxing	
Farming type	SA	CA	SA	CA	SA	CA	SA	CA
No. of families	67	59	73	63	60	52	68	60
No. of species	191	153	200	173	166	122	172	137
No. of individuals	7,333	4,605	9,230	5,463	6,521	8,100	6,290	5,978
Shannon's Index	2.90	2.59	2.91	2.59	2.98	1.98	2.84	2.31
Simpson's Index	0.84	0.83	0.87	0.84	0.89	0.75	0.85	0.78
Pielous's Index	0.55	0.51	0.55	0.50	0.58	0.41	0.55	0.47
Margelef's Index	21.4	18.1	21.9	20.1	18.9	13.6	19.7	15.8

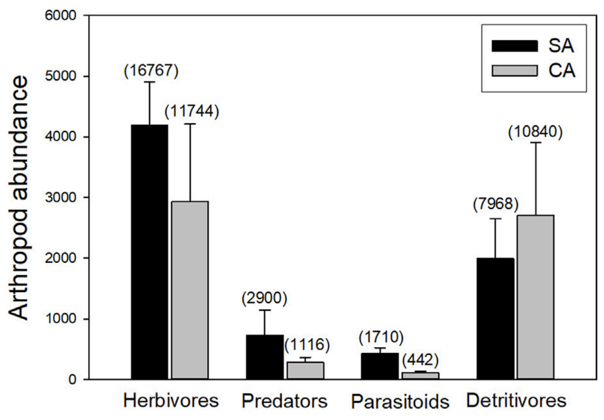

FIGURE 5
Comparison of arthropod abundance between SA and CA farming. The total arthropod abundance is shown in the parentheses.

represented by long-jawed orb weavers (Tetragnathidae), orb-weaver spiders (Araneidae), Miridae, and Coccinellidae. The detritivores guild represented 35.3% of the total arthropod abundance and was mainly composed of chironomids and some collembolans. Finally, parasitoids accounted for 4.0% of the total abundance and were mainly represented by Mymaridae and Pteromalidae. According to the GLMM, the abundance of herbivores (AIC = 498.8, $p < 0.001$), parasitoids (AIC = 334.4, $p < 0.001$), and detritivores (AIC = 478.2, $p < 0.001$) presents the best model when only the farming type was assigned as the fixed effect, while the predators reveal the best model when the farming type, landscape, and their interaction were assigned as the fixed effects (AIC = 381.3, $p < 0.05$). Moreover, the abundance of herbivores, parasitoids, and predators is higher under SA farming but not detritivores (Figure 5).

4 Discussion

We recorded a total of 445 morphospecies of arthropods in the paddy field of northern Taiwan, which is higher than in other studies of the paddy field in the Philippines (Heong et al., 1991; Dominik et al., 2017). Overall, the abundance of arthropods in SA farming was higher than that of CA farming (Table 2). Conventional agroecosystems are not easily colonized by arthropod species as there is typically a lack of flora diversity (monocropping), and these areas are heavily disturbed (Brown, 1991; Benton et al., 2003). SA farming (eco-friendly agriculture) has a higher abundance of arthropods because of the limited use of pesticides.

Hemiptera, Thysanoptera, and Diptera are the three most dominant arthropod taxa in our study sites. Hemiptera, mostly Delphicidae, Cicadellidae, and Aphidae, and Thysanoptera are known major pests of rice in Taiwan (classified as herbivores). The abundance of these two taxa is significantly higher under SA farming compared to that in CA farming. This result is predictable because some major pesticides applied in the paddy field are specific to hemipteran and thysanopteran pests. However, another dominant group, Diptera (specifically Chironomidae), is classified as detritivores in this study, whose abundance is higher under CA farming. Their larvae are aquatic and feed on organic humus and algae in farmlands, ditches, and semi-aquatic environments (Stevens et al., 2006). Chironomids can endure water pollution and do not require good habitat quality (Al-Shami et al., 2010). In the early stages of rice farming, paddy fields are full of water. At this time, a large number of chironomids inhabit the paddy fields. They usually occur in the early stage of the paddy field, in which the pesticide spray is less compared to the later stage of the paddy field. This may cause some effects on chironomids by pesticides. On the other hand, Diptera abundance may be slightly affected by certain landscape factors, including ditch coverage. In this study, Chironomidae represented nearly half of the total arthropod abundance in the LdCA, which possess some coverage of ditches (Figure 2). The distance to the nearest waterbody also affects the distribution of chironomid populations (Delettre and Morvan, 2000). However, this phenomenon is not verified statistically and needs further study.

In this study, we also have found that the abundance of parasitoids, specifically parasitoid wasps of Hymenoptera, is higher in paddy fields under SA farming methodologies. This has seldom been mentioned in previous studies. The importance of other natural enemies in paddy fields has been well-documented, such as spiders and ground beetles (Tsutsui et al., 2016; Russell et al., 2017). These generalists play an important role in the suppression of pest populations (Settle et al., 1996). However, the significance of specialists, like parasitoid wasps, deserves more attention. Parasitoid wasps search for specific host species and effectively decrease the population of that host, which may or may not be considered a pest. The most dominant parasitoids in this study are Mymaridae, which are the major parasitoids of hemipterans (Jacob et al., 2006; Mutitu et al., 2013). It is observed that the most dominant herbivores in the paddy field are hemipterans. Both ecological guilds are significantly increased in the sustainable farming type (Birkhofer et al., 2016).

Other factors of the farming type may also be beneficial to the arthropod community, like loosening planting density. Many previous studies have pointed out that the rice planting density and interval are related to the field's hemipteran population and disease occurrence (Denno and Roderick, 1991; Ishii-Eiteman and Power, 1997). Moreover, the density of rice plants may affect an arachnid's ability to inhabit the paddy because dense planting would make web building more difficult, and the prey could remain hidden more easily (Foelix, 2011; Butt and Xaaceph, 2015). Roitberg (2018) also suggested that dense field planting may increase the difficulties for parasitoid wasps to find their host.

In this study, the surrounding landscape seems to not have any overall effect on the arthropod community, inferring that a simplified landscape may weaken the effect of the landscape. Dominik et al. (2017) suggested that arthropod composition is extremely different among different landscapes, which is less significant in our study. However, the sampling sites of Dominik et al. (2017) are separated by about 100 km, which makes the surrounding landscape completely different, including the terrain and flora. These abiotic and biotic differences cause the varied arthropod composition. In contrast, our four sampling sites are all located in the Lanyang Plains, which is an important area of rice production in northern Taiwan since the 18th century. After a long history of reclaim, more than 11,100 ha of area are paddy fields currently (AFA, 2023). The native vegetation has been removed in this area, which is a simplified landscape. The sampling areas of this study are separated by merely more than 1 km, which suggests that the arthropods moderately share the same surrounding landscape. The simplified landscape may result in a decrease in arthropod diversity; on the other hand, it highlights the importance of sustainable farming in the paddy field. More biodiversity in an agricultural ecosystem will bring more ecological service to humans. The arthropod diversity is more vulnerable in a simplified landscape without abundant vegetation. Moreover, the neighborhood effects of conventional farms cause negative effects on the sustainable farms nearby. We suggest that the policy of payments for ecosystem services (PES) should be promoted in Lanyang Plains to maintain the arthropod diversity.

5 Conclusion

In conclusion, our work suggests that the effects of the sustainable farming type on arthropod communities in paddy fields are beneficial to certain arthropod taxa, such as Hemiptera (major herbivores), Araneae (major predators), and Hymenoptera (major parasitoids). The spraying of pesticides mainly focuses on the hemipteran prey, and the major host of parasitoid wasps collected by this study is also hemipterans. To properly analyze and compare arthropod diversity and abundance with factors such as farming methodology and landscape, some important steps must be taken. First, a specific understanding of the diversity and taxonomic makeup of the ecosystems that are being examined must be developed. Once this is understood, taxa that are known to be more sensitive to factors that are being compared and focused on should be selected. Second, different farms located in varied landscapes need to be compared to understand the effect of landscapes on the arthropod community.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material.

Ethics statement

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

Author contributions

Conceptualization: J-HC, Y-CL, and M-MY; methodology and software: J-HC and M-CC; data collection and curation: J-HC and Y-CL; writing—original draft preparation: J-HC and Y-CL; supervision: Y-CL and M-MY; funding acquisition: M-MY. 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.

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Incorporating phylogenetic conservatism and trait collinearity into machine learning frameworks can better predict macroinvertebrate traits

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In the face of rapid environmental changes, understanding and monitoring biological traits and functional diversity are crucial for effective biomonitoring. However, when it comes to freshwater macroinvertebrates, a significant dearth of biological trait data poses a major challenge. In this opinion article, we put forward a machine-learning framework that incorporates phylogenetic conservatism and trait collinearity, aiming to provide a better vision for predicting macroinvertebrate traits in freshwater ecosystems. By adopting this proposed framework, we can advance biomonitoring efforts in freshwater ecosystems. Accurate predictions of macroinvertebrate traits enable us to assess functional diversity, identify environmental stressors, and monitor ecosystem health more effectively. This information is vital for making informed decisions regarding conservation and management strategies, especially in the context of rapidly changing environments.

KEYWORDS

biodiversity, global change, sustainable development, phylogenetic tree, trait

1 Introduction

1.1 Freshwater biodiversity and sustainable development

Freshwater biodiversity provides vital natural resources for humans in economic, cultural, aesthetic, scientific, and educational terms. Its conservation and management are of paramount importance to the interests and well-being of all humans, nations and governments. However, despite conservation efforts, freshwater biodiversity is experiencing rapid declines at regional or global scales, due to increasing intensity of disturbances from human activity, biotic pressure, and environmental changes (Mouillot et al., 2013). As a consequence, biodiversity loss poses a threat to the sustainability of ecological processes and the provision of ecosystem services (Renault et al., 2022). Thus, biodiversity challenges become one of the most important issues in the Sustainable Development Goals (SDGs). Among the SDGs, the sustainable use of marine and aquatic resources and terrestrial ecosystems are most closely related with biodiversity. Biodiversity is an important indicator to evaluate the sustainable development of human society since it provides the essential resource for human surviving. The balance between biodiversity conservation and utilization is crucial for sustainable development.

Documenting losses of biodiversity, diagnosing their causes, and finding solutions are key issues in freshwater ecology (Strayer and Dudgeon, 2010). Traditional freshwater biodiversity studies mainly focused on taxonomic diversity. Although some kinds of new technologies were implemented, such as meta-barcoding (Serrana et al., 2018) and single-molecule real-time (SMRT) sequencing (Zhang et al., 2020), which obtain species taxonomic annotation by aligning environmental sequences to reference databases, analyses of these new methods still primarily focused on species diversity. It is argued that taxonomic diversity alone cannot explain the observed patterns that respond to environmental disturbances (Gagic et al., 2015).

1.2 Biological trait, functional diversity, macroinvertebrates, and global change

Despite a range of conservation measures being implemented, biodiversity loss continues to occur widely in the context of habitat destruction (Visconti et al., 2011) and global changes (Maclean and Wilson, 2011). So, it cannot wait to develop a method for quantifying and predicting the impact of disturbance on biodiversity patterns (Mouillot et al., 2013).

It has been confirmed that the response to disturbances and other environmental conditions depends on the traits (including life history, behavior, physiology, morphology, ecology, environmental preferences, and tolerances or sensitivities) of the species (Mouillot et al., 2013; Gagic et al., 2015). Functional traits have been shown to serve as important characterizations of community or ecosystem function in response to various disturbances (Tilman et al., 1997; Petchey et al., 2004; Verberk et al., 2013). Furthermore, researches based on species traits can provide more information than studies merely on classical taxonomy (Barnett et al., 2007; Luo Q. et al., 2022). So, the focus of related research has also shifted from taxonomic diversity to functional diversity (Renault et al., 2022).

Macroinvertebrates, characterized by their rich diversity, wide distribution, and environmental sensitivity, have been long utilized to study ecological responses, such as hydrological disturbances, based on their functional traits (Townsend et al., 1997). Until now, studies on macroinvertebrates' functional diversity have kept exploding for more than 20 years. Recently, research has delved into the typical number of traits considered for estimating functional diversity and the specific traits commonly used for index calculation (Ao et al., 2023). Some studies summarized the macroinvertebrate trait databases that have already been produced (Kefford et al., 2020). These research foundations offered the possibility of constructing a relatively well-developed framework based on macroinvertebrate traits to quantitatively predict the impact of disturbance on biodiversity patterns. However, acquiring comprehensive trait datasets for organisms demands substantial sampling efforts, consequently leading to frequent occurrence of missing data.

1.3 Limitation of current applications and our intention

We propose a conceptual framework that integrates machine learning, phylogenetic conservatism, and trait collinearity to address the paucity of biological trait data for freshwater macroinvertebrates (Kefford et al., 2020). This lack hinders our understanding of functional diversity and the effects of global change. To predict missing traits, we propose a machine-learning model with predictors of phylogenetic information and trait collinearity. By incorporating these predictors, we can improve predictions by accounting for 1) phylogenetic distances among species and 2) associations among traits within species or taxonomic groups. This advance contributes to understanding functional diversity, assessing the impacts of global change, and guiding conservation and management efforts for freshwater ecosystems. In the position paper, we then discuss the current state and our proposed framework for addressing missing trait data.

2 Current state to address the lack of trait database

2.1 Current frameworks

By addressing the lack of biological trait data, the current frameworks rely on the selection of traits available in freshwater macroinvertebrates (Ao et al., 2023). This limitation can be overcome by predicting biological traits based on phylogenetic conservatism and using mathematical tools such as machine learning (Debastiani et al., 2021). Phylogenetic conservatism suggests that closely related species share similar trait values due to their shared evolutionary history. Machine learning algorithms analyze large datasets and extract patterns from complex biological data. By integrating machine learning into the framework, researchers can estimate missing trait values based on known trait values of closely related species. By leveraging machine learning's ability to identify patterns and correlations among traits, this approach can enable researchers to gain insights into the ecological implications of these traits and their impact on ecosystem dynamics.

2.2 Phylogenetic conservatism

As species traits are integrated as a part of a hierarchically structured phylogeny (Felsenstein, 1985), and given the propensity for greater trait similarity among closely related species compared to those more distantly related (Pagel, 1999), coupled with the conservatism of the phylogeny, it gives the theoretical basis for linking phylogenetic information and traits. So, some data imputation methods encompassed or based on phylogenetic information had been developed, such as Phylopars, which utilizes phylogeny and allometric relationships among traits (Bruggeman et al., 2009), and Phylogenetic Eigenvector Maps (PEM) (Guenard et al., 2013).

The methods that take phylogenetic information of species into account have been considered to be potentially powerful ways to complete trait data imputation (Swenson, 2014). Debastiani et al. (2021) proposed a framework that integrates phylogenetic information with imputation methods employing missForest and assessed the performance of the missForest algorithm for imputing species trait values by incorporating phylogenetic information. The results showed that the inclusion of phylogenetic vectors into the missForest algorithm leads to a substantial improvement in the imputation of missing values under some certain conditions. It demonstrates the promising application of incorporating phylogenetic conservatism into machine learning frameworks to predict macroinvertebrate traits.

2.3 Machine learning in ecology and environmental sciences

Machine learning methods possess a robust nonlinear modeling capability, making them particularly effective in detecting and describing structural patterns within large datasets, as well as providing relative importance values among independent variables (Biau and Scornet, 2016). They had been widely applied for species distribution pattern prediction and constrained environmental factors detection in community-level studies in ecology and environment sciences (Smith and Carstens, 2020). The prediction function made machine learning methods being used in extremely wide areas such as satellite data processing (Kim et al., 2014), weather and climate prediction (Watson-Parris, 2021), air quality forecasting (Fu et al., 2023), and monitoring of snow, ice, and forests (Luo J. et al., 2022). The nonlinear modeling capability of machine learning methods made them powerful in genomic prediction for non-linear traits. Song et al. (2023) had performed Bayesian threshold model and machine learning methods to improve the accuracy of genomic prediction for ordered categorical traits in fish. Fish egg color was predicted with both methods. Machine learning methods showed higher prediction accuracies than Bayesian methods. In wheat leaf traits monitoring studies, machine learning methods could provide comparatively precise and robust prediction of leaf parameters based on high-resolution satellite imagery data (Jamali et al., 2023). Li et al. (2020) extended those methods to population genetic studies. The relative importance was used to determine environmental factors that drive adaptive divergence.

3 Proposed framework with phylogenetic conservatism, trait collinearity, and machine learning

3.1 The proposed framework

We propose an innovative framework that combines phylogenetic conservatism, trait collinearity, and machine learning to revolutionize the prediction and understanding of biological traits (Figure 1). The analysis of an incomplete macroinvertebrate trait set using this framework consists of the following steps: (1) View the data set and clarify missing data. (2) Get the phylogenetic distances between related species based on phylogenetic data. (3) Deduce the value of the missing trait by phylogenetic distances through machine learning. (4) Get the co-occurrence relationships between related traits and add it to machine learning to estimate the deduced value. By incorporating the construct of trait collinearity along with known features such as phylogenetic conservatism and machine learning, this integrated framework enhances our ability to accurately estimate missing trait values. Its applications span across ecology, evolution, and conservation biology, deepening our understanding of trait evolution, functional diversity, and the impacts of global change. Furthermore, the framework informs conservation and management strategies by highlighting traits crucial for species resilience. Through this integration, valuable insights into trait variation and its ecological and evolutionary significance are unlocked.

3.2 Trait collinearity

The diversity in functional traits within species is shaped by both genetic differentiation and phenotypic plasticity (Albert et al., 2010). Additionally, it mirrors the evolutionary past and the species' adjustments to environmental conditions (Diaz and Cabido, 2001). Given the intricate nature of the origins of functional diversity, employing a multivariate framework that combines the phylogenetic aspects of biodiversity with trait-based methodologies becomes crucial (Felsenstein, 1985). To complete trait datasets, the use of data imputation methods with phylogenetic information of species is considered a potentially effective approach until more accurate trait information is obtained (Swenson, 2014). The foundation for linking evolutionary traits to traits lies in the recognition that species traits are interrelated rather than

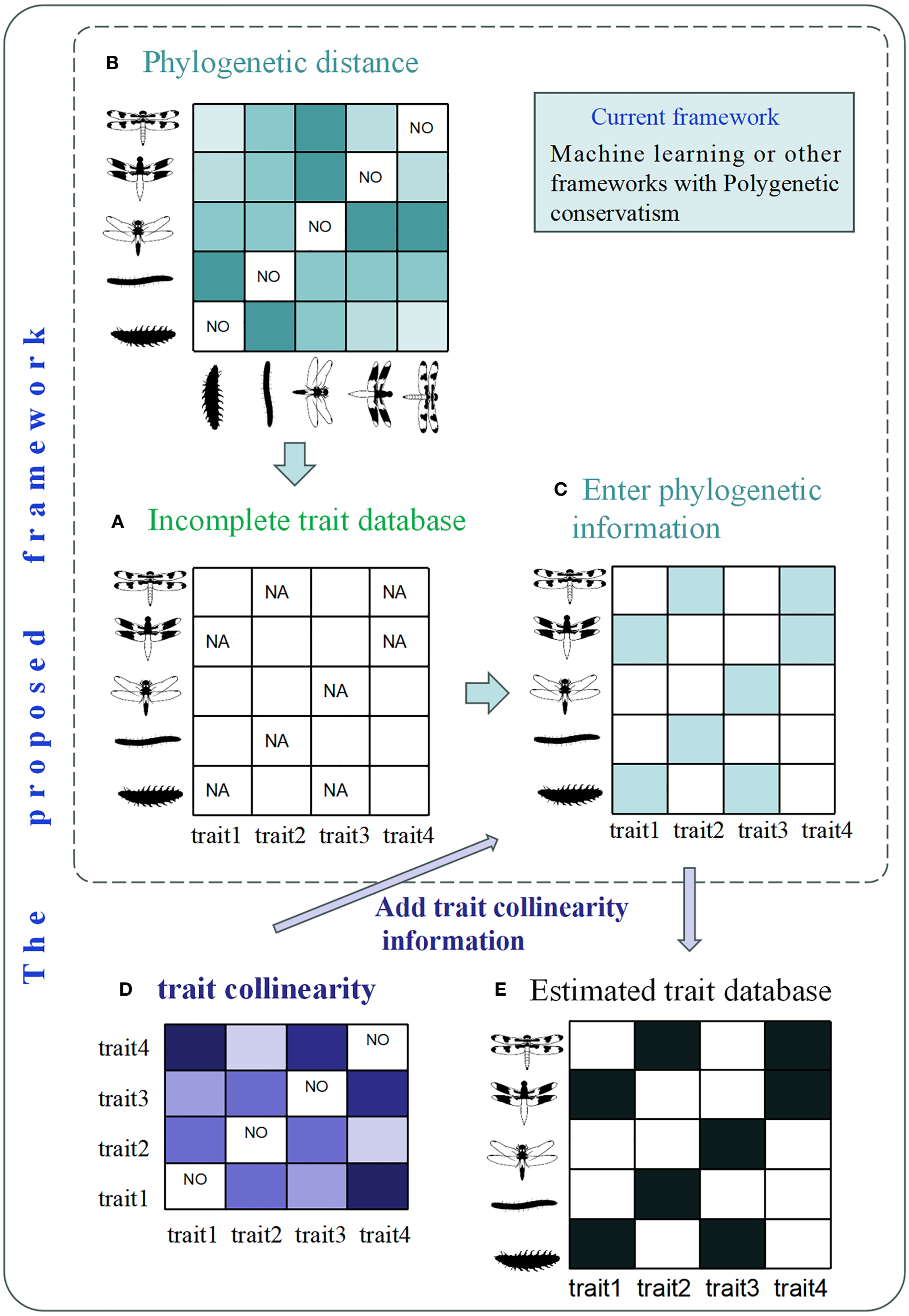

FIGURE 1
Current framework (with phylogenetic data) and prospect framework (with addition of trait collinearity information): **(A)** analysis of incomplete trait sets in macroinvertebrate, NA representing missing trait information. **(B)** Phylogenetic distance between species. **(C)** The value of the missing trait is deduced by adding phylogenetic data through machine learning (light blue data box). **(D)** Co-occurrence relationships between traits. **(E)** The inclusion of information on trait collinearity makes the derived values (Black data box) of missing traits more reliable. Silhouettes were obtained from phylopic.org under the public domain licenses.

independent and they are embedded within a hierarchical phylogenetic tree (Felsenstein, 1985). Studies of functional variation are based on the idea of functional trait covariation (Grime et al., 1997), a model of covariation that can define general ecological strategies (Reich et al., 2003). The study of functional variation has been more widely explored in the field of botany than in aquatic organisms. For example, covariation patterns among leaf traits (such as the leaf economic spectrum) have been linked to strategies for efficient resource acquisition and resource conservation (Wright et al., 2004).

4 Summary

Here, we propose integrating machine learning, phylogenetic conservatism, and trait collinearity into a conceptual framework.

The lack of biological trait data for freshwater macroinvertebrates impedes our exploration of functional diversity and understanding of global change impacts (Kefford et al., 2020). Thus, there is a global effort to develop methods for predicting missing traits. To bridge this gap, we recommend incorporating trait collinearity into the existing framework that already considers machine learning and phylogenetic conservatism. Trait collinearity involves the correlation or association of certain traits within a species or taxonomic group. By integrating this concept, we can enhance our ability to predict missing traits. Machine learning algorithms are effective at extracting patterns from complex biological data, making them valuable tools. By training these algorithms with existing trait data and incorporating phylogenetic information, predictive models can estimate missing traits based on known trait correlations. This approach leverages the similarity of trait values among closely related species due to phylogenetic conservatism. Including trait collinearity in the framework would improve predictions by considering interrelationships among traits within species or taxonomic groups. Accounting for these associations enhances the accuracy of trait predictions and provides a comprehensive understanding of functional diversity. By integrating trait collinearity and phylogenetic conservatism into machine learning models, we can leverage available data to predict missing biological traits in freshwater macroinvertebrates. This advancement significantly contributes to our understanding of functional diversity, enables better assessments of global change impacts, guides conservation efforts, and informs effective management strategies for freshwater ecosystems, promoting their long-term sustainability.

Author contributions

SL: Conceptualization, Funding acquisition, Software, Writing – original draft, Writing – review & editing. QL: Conceptualization, Software, Writing – original draft. RL: Conceptualization, Writing – original draft, Writing – review & editing. BL: Conceptualization, Writing – original draft, Writing – review & editing.

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Dynamic patterns of beta diversity in the Anthropocene: incorporating moderators into dissimilarity-based models

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biodiversity, ecosystem functioning, ecological processes, generalized dissimilarity model, Mantel tests

1 Introduction

Biodiversity plays a crucial role in enhancing resource use efficiency, ecosystem functioning, and stability of ecological processes in the Anthropocene (Balvanera et al., 2006; Cardinale et al., 2006). However, human activities and biological invasions have led to widespread loss of biodiversity on Earth, posing threats to aspects such as food and medicine supply and ecosystem functioning regulation (McGeoch et al., 2010; Diaz et al., 2019). Therefore, accurately measuring biodiversity and predicting its temporal and spatial changes have been central research focuses in ecology (Solow and Polasky, 1994; Cardinale et al., 2012). Through continuous efforts by ecologists, methods for measuring biodiversity and analytical techniques have been constantly evolving and improving (Solow and Polasky, 1994; Legendre and Legendre, 2012). The development and refinement of these methods have enhanced our scientific understanding of life diversity on Earth and facilitated the conservation and management of biodiversity.

Among numerous methods for measuring and analyzing biodiversity, the dissimilarity-based models [DM; e.g., the Mantel tests (MT) and generalized dissimilarity model (GDM)] are the most commonly used for analyzing and predicting the spatiotemporal turnover patterns of communities (Xu et al., 2022). The Mantel test can assess the linear correlation of community changes with environmental variation (Mantel, 1967). Smouse et al. (1986) extended the statistical methods of MT, allowing for multivariate regression and correlation analysis, thus enhancing the applicability and flexibility of MT. Blanchet et al. (2008) discussed the use of forward selection in MT to identify the most important explanatory variables, improving the interpretability and explanatory power of MT results. GDM can explore the non-linear regression between community distance and ecological distance (e.g., environmental and geographic distances), detecting the extent of community changes along environmental gradients and informing us about the contribution of each important environmental variable (Ferrier et al., 2007). GDM's applications in the analysis of biodiversity time series data (Dornelas et al., 2014) and the assessment of regional biodiversity (Ferrier et al., 2007) fully demonstrate its value in predicting spatiotemporal turnover patterns of community composition, enhancing our understanding of biodiversity patterns and processes. However, GDM may involve uncertainties in handling diversity data,

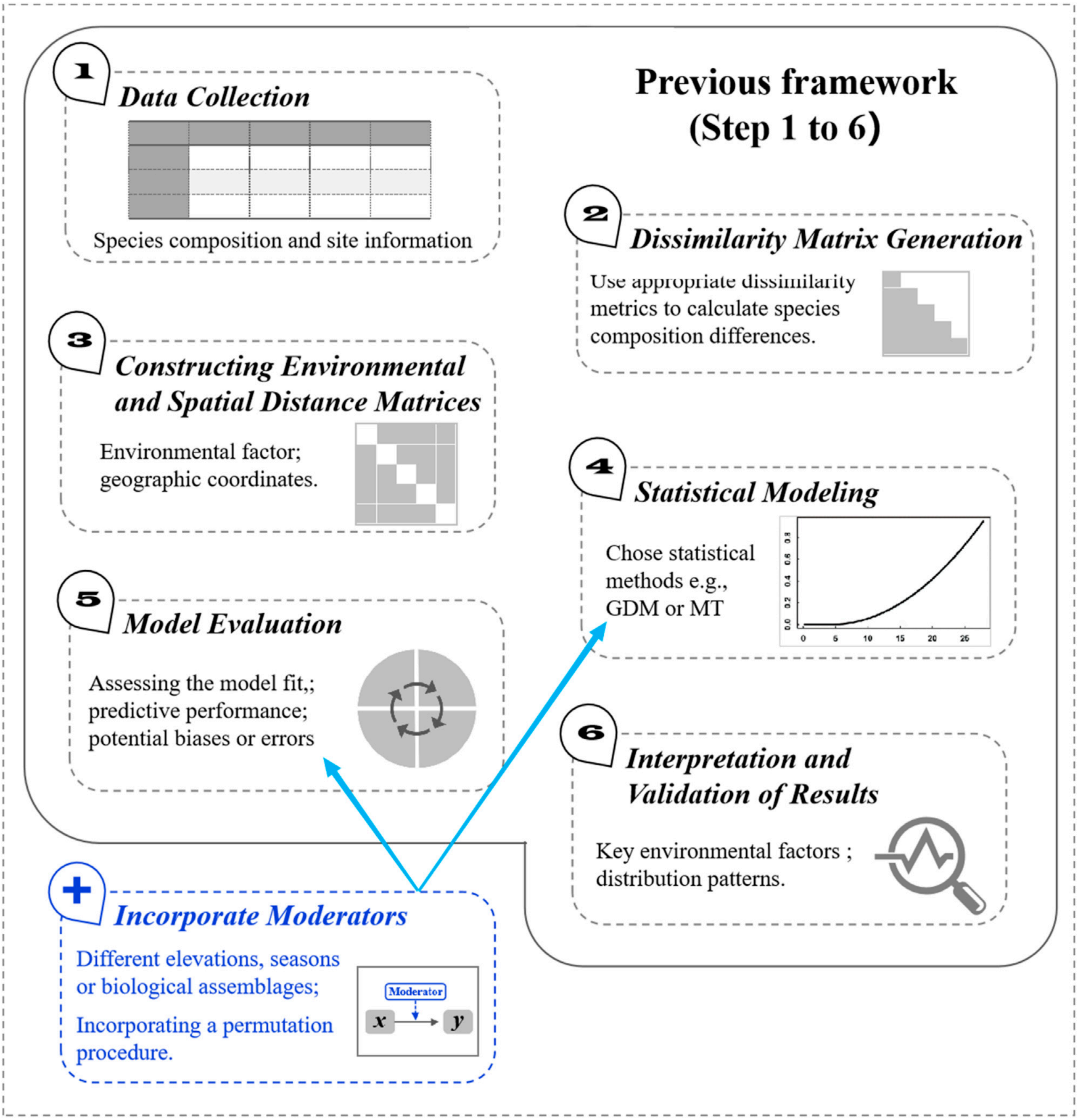

FIGURE 1
Flow chart to show the analytic procedures (Innovations in this study are marked in blue).

which can arise from spatial autocorrelation, data gaps, or measurement errors (Woolley et al., 2017).

In this opinion article, we propose a conceptual framework by expanding the capabilities of DMs to incorporate mediators, aiming to overcome the intrinsic limitations that hinder the exploration of dynamic patterns in beta diversity with robust empirical support. While existing DMs excel at unveiling associations between community composition and environmental or spatial factors, they typically fall short in directly identifying and elucidating the roles of moderators and their underlying mechanisms. Researchers often rely on independent models for various moderating factors (e.g., different geographic regions, seasons, or biological assemblages), rather than integrating these moderating influences into a unified analytical model (Ferrier et al., 2007). Mere numerical comparisons among the outcomes of these independent DMs do not inherently convey the significance of the moderating factors. Therefore, our approach responds to the pressing need for models that align with our proposed conceptual framework, offering a comprehensive understanding of the intricate ecological mechanisms at play within beta diversity patterns and addressing this research frontier with rigor and innovation.

2 Integration of moderators into the model

The comprehensive DM workflow consists of six key steps (Figure 1). First, data collection (Step 1) entails the gathering of biodiversity data from various locations, including site-specific details and species composition information. Next, a dissimilarity matrix (Step 2) is generated, employing appropriate dissimilarity metrics like the Bray-Curtis distance to quantify the differences in species composition across these locations. To delve deeper into ecological patterns, environmental data (e.g., temperature, precipitation, and habitat characteristics) and geographic coordinates (latitude and longitude or other spatial identifiers) are gathered for constructing environmental and spatial distance matrices (Step 3), effectively measuring disparities in environmental factors and spatial distances. Subsequently, statistical modeling techniques (Step 4) are applied, employing DM methodologies. Once the modeling analysis is complete, model evaluation (Step 5) comes into play, encompassing the assessment of the constructed DM, which includes evaluating model fit, predictive performance, and potential biases or errors, thereby ensuring the reliability and integrity of the analysis. Finally, results are interpreted (Step 6) to decipher how environmental factors influence species composition disparities and how spatial distance shapes species distribution patterns.

In the phase of applying the methodologies as they stand today, DMs construct the relationship between biological dissimilarity and environmental and/or spatial distance in the following manner:

$$y_{a,b} = \sum f_i\left(x_{i,a}, x_{i,b}\right) \tag{1}$$

where the function $f_i\left(x_{i,a}, x_{i,b}\right)$ serves as a versatile tool capable of capturing either linear or nonlinear effects arising from the distance between the variable x_i in samples a and b. These variables x represent a wide range of factors, including but not limited to intercepts, environmental conditions, and spatiotemporal factors. The primary objective is to unveil the intricate relationships that underpin beta diversity (represented as y) between two distinct samples, which may vary across different regions or seasons. This modeling process allows us to decipher the complex interplay between ecological variables and beta diversity patterns, offering valuable insights into the dynamics of biodiversity in various contexts.

Incorporating moderators into the DMs represents a significant advancement in our understanding of ecological relationships. In this context, the model formulates the intricate relationship between biological dissimilarity and environmental and/or spatial distance as follows:

$$y_{a,b} = \sum_i \sum_j f_{i,j}\left(x_{i,a}, x_{i,b}, z_j\right) \tag{2}$$

where the function $f_{i,j}\left(x_{i,a}, x_{i,b}, z_j\right)$ assumes a pivotal role of the moderator z_j and these moderators represent various factors such as differing geographical regions and distinct biological assemblages. These moderators serve as dynamic agents, introducing influences that intricately interact with variables x. In doing so, they modulate and fine-tune the effects of x on beta diversity (denoted as y). This innovative approach enables a more comprehensive exploration of the multifaceted relationships underlying biodiversity patterns, allowing us to decipher how different areas and biological assemblages influence the dynamics of beta diversity across diverse ecosystems.

Regarding the steps dedicated to model fitting and the critical phase of significance testing, our approach harmonizes seamlessly with the established framework. The process of model fitting remains consistent with the previous one when employing this framework. The model fitting can be achieved using the Iteratively Re-weighted Least Squares (IRLS) algorithm, However, it's in the domain of significance testing that our method introduces a valuable innovation.

While staying true to the core principles of the original DMs, we augment our approach by incorporating a permutation procedure that is different from the original procedure. To overcome the problem of lack of independence between site pairs, the original significance testing is performed using a random permutation procedure, which involves comparing the deviance explained by the fitted model with the deviance calculated when either individual or all predictor variables are randomly shuffled among the samples (Mokany et al., 2022). Rather than that, the procedure proposed in this article involves the systematic reshuffling of sample order, encompassing sites or time points, within a single matrix at each level of the moderator. For example, when taking elevation as a moderator, the samples could be re-permuted according to the elevation at which the samples were collected to obtain different matrices corresponding to each elevation. These matrices are then used to assess the significance of the effect of variables x on beta diversity at different elevations. This innovative permutation methodology equips us with a potent tool to rigorously assess the statistical significance of our findings. Importantly, it achieves this while preserving the fundamental integrity of the model fitting process, ensuring that our results are robust and reliable. By combining the strengths of the original DM with this novel permutation technique, we enhance the depth and precision of our ecological analyses, advancing our capacity to unveil critical insights into the complex relationships shaping biodiversity patterns across diverse ecosystems.

3 Summary

Expanding upon our data collection methods, which encompass field surveys and remote sensing, our proposed framework plays a pivotal role in advancing our understanding of dynamic beta-diversity patterns in the Anthropocene. This progress is achieved by enhancing the capabilities of DMs through the incorporation of moderating variables, including but not limited to those related to spatiotemporal factors and biological traits. These moderating variables exert significant influence over the intricate interplay between environmental and biotic dissimilarities, ultimately shaping the dynamics of beta diversity. The innovation embedded within this conceptual framework not only amplifies the applicability of DMs but also propels scientific inquiry forward with a solid foundation of empirical evidence. Consequently, this advancement holds significant potential for strengthening the development of dependable management and conservation strategies in a rapidly changing world. In doing so, it contributes to the sustainability of our ecosystems and fosters a harmonious coexistence between humans and the environment.

Author contributions

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Assessing the invasion risk of *Chelydra serpentina* in China under current and future climate change scenarios

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Chelydra serpentina, a species introduced to China for aquaculture purposes, is commonly found in its natural habitats within the country. The invasion of *C. serpentina* poses potential threats to both the biodiversity of China and human health. The potential distribution of *C. serpentina* has been simulated using the species distribution model – MaxEnt, incorporating global distribution data, climate, and land cover variables. Our simulations encompasses both current conditions and four future climate change scenarios. Currently, the potential distribution is concentrated in central, eastern, and southeastern regions of China, with the central and eastern regions facing the highest risk of invasion. Under future climate change scenarios, the distribution area may expand by 30–90%, and multiple provinces will face a more severe threat of invasion. This study presents the inaugural simulation of the potential invasion range of *C. serpentina* under current climatic conditions. Moreover, it reveals that climate change is likely to contribute to the expansion of its invasive range, thus furnishing a reference foundation for scientific prevention and control measures. We propose integrating citizen science and eDNA technologies into species monitoring to enhance the efficiency of detecting invasive species. This research has filled the gap in the research on the invasive distribution range of *C. serpentina* in China and globally, while also providing novel perspectives on the invasion control of this species.

KEYWORDS

***Chelydra serpentina*, invasive alien species, species distribution models, climate change, potential distribution, management**

1 Introduction

Globally, non-native freshwater turtles have been intentionally or unintentionally introduced into various habitats (Sung et al., 2021), causing damage to local biodiversity and ecosystems through competition (Díaz-Paniagua et al., 2011), hybridization (Ueno et al., 2021), and the spread of parasites (Mendoza-Roldan et al., 2020) and diseases (Bosch et al., 2015). To prevent the further spread of invasive alien species (IAS), employing species distribution models (SDMs) to analyze the current and future ranges of IAS can provide a scientific basis for decision-making (Bertolino et al., 2020).

It is expected that the global surface temperature will continue to increase at least until the middle of the century (Masson-Delmotte et al., 2021). Climate change and biological invasions occur simultaneously in both space and time, and there is a potential for synergistic effects in the future (Stephens et al., 2019). The persistent climate change poses an escalating threat to biodiversity and ecosystems (Watson et al., 2019). Forecasts suggest that global warming will alter the geographical ranges of various species (Duan et al., 2016). The survival of species in response to climate change will likely depend on their dispersal capabilities (Capinha et al., 2013). Species with narrow ecological niches and limited dispersal abilities, including many endangered species, are significantly more vulnerable to environmental changes (Malcolm et al., 2006) compared to species with extensive dispersal abilities (Slatyer et al., 2013) like IAS. IAS are often better adapted to local conditions, outcompeting slower-spreading species and potentially leading to their extinction (Urban et al., 2012).

China's complex terrain and climatic diversity contribute to its abundant biodiversity compared to other countries at similar latitudes (SEP A (State Environmental Protection Administration), 1998). China has identified over 660 IAS (Xian et al., 2018), including four species from the Testudines order: pond slider turtle (*Trachemys scripta*), Florida softshell turtle (*Apalone ferox*), alligator snapping turtle (*Macrochelys temminckii*), and common snapping turtle (*Chelydra serpentina*) (Ji, 2023). The original natural range of *C. serpentina* extends from the southeastern region of Alberta, Canada, eastward in the United States to the east of the 105th meridian, and southwards to the Gulf Coast (Ernst and Lovich, 2009). *C. serpentina* has been introduced in various countries across Asia (including China, Japan, Singapore), Europe (Germany, the Netherlands, France, Spain), and South America (Mexico, Honduras, Costa Rica, Panama, Ecuador) primarily through the pet and food trade (Koo and Sung, 2020). Around 1997, China began introducing *C. serpentina* due to its rapid growth, high egg production, substantial meat yield, simple feeding requirements, and low susceptibility to disease. This led to rapid development in aquaculture, and in 2005, the Ministry of Agriculture of the People's Republic of China endorsed this species for aquaculture promotion (Liu et al., 2007). *C. serpentina* is frequently discovered in the natural habitats of China and has been featured in various online news outlets (Liu et al., 2021). In the region of Hong Kong, *C. serpentin*a has also been witnessed on no less than 10 occasions (Sung et al., 2021). Therefore, we hold the belief that China is currently confronted with a significant risk of *C. serpentina* invasion. As apex predators, these formidable creatures exert a significant cascading effect on freshwater ecosystems (Wilbur, 1997; Lovich et al., 2018; Garig et al., 2020). Even their brief visits can induce substantial changes in freshwater communities (Garig et al., 2020).

SDMs are statistical models that utilize observed distribution data to infer species ecological requirements and map their potential distribution (Austin, 2002). They are widely used to quantify species responses to climate change (Araújo et al., 2011; Newbold et al., 2020). This study aims to simulate the potential global and China-specific distributions of *C. serpentina* by utilizing existing records of its occurrence and high-resolution data on climate warming and water bodies. The study sets forth three distinct research objectives: (1) Assessing the potential distribution of *C. serpentina* in both current and future climatic conditions; (2) Spatially delineating the contraction and expansion patterns within the distribution range of *C. serpentina*; (3) Identifying the principal environmental variables that strongly correlate with the distribution of *C. serpentina*. This study presents the inaugural simulation of the potential invasion range of *C. serpentina* under current climatic conditions. Additionally, it reveals the impact of climate change on the invasive range of *C. serpentina*, thus furnishing a reference foundation for scientific prevention and control measures. Moreover, based on the biological characteristics of *C. serpentina*, suggestions for conducting field investigations have been proposed to enhance monitoring efficiency. This study has filled the gap in the research on the invasive distribution range of *C. serpentina* in China and globally, while also providing novel perspectives on the invasion control of this species.

2 Materials and methods

2.1 Occurrence and environmental data

We obtained the global occurrence records for *C. serpentina* from the Global Biodiversity Information Facility (GBIF), accessed on 23 May 2023 (GBIF, 2023). Any records that fell outside the range of bioclimatic variables were excluded. In order to reduce the impact of sampling bias, we performed spatial thinning using the spThin R package (R Version 4.3.0), with a minimum distance of 10km between pairs of sites (Aiello-Lammens et al., 2015). In the end, we obtained 7,897 occurrence records of *C. serpentina* for our study, of which 97.34% were within the original range (Figure 1). We utilized global occurrence data for model calibration because relying solely on occurrence data from native habitats may lead to an underestimation of potential distribution areas. This is primarily because it overlooks the essential survival strategies species employ to mitigate the effects of environmental changes. These mechanisms include exploiting microclimates, regulating body temperature, adjusting life history traits, and exhibiting evolutionary adaptations (Bonebrake et al., 2014; Faye et al., 2014; Bush et al., 2016). This is particularly relevant for IAS, which often exhibit heightened adaptability (Kolar and Lodge, 2001).

Nineteen global bioclimatic and elevation variables were sourced from the WorldClim databas (Hijmans et al., 2005), derived from the Coupled Model Intercomparison Project Phase 5 (CMIP5). The current climatic variables are based on the long-term average data for 1960–1990. As turtles are aquatic organisms, land cover data of Chen et al. (2022) were utilized to generate data on water bodies and distance from water bodies. The current land cover variables use 2015 data. Water bodies were represented using binary data (1 for water, 0 for non-water) (Gábor et al., 2022), while the distances from water bodies were represented using continuous

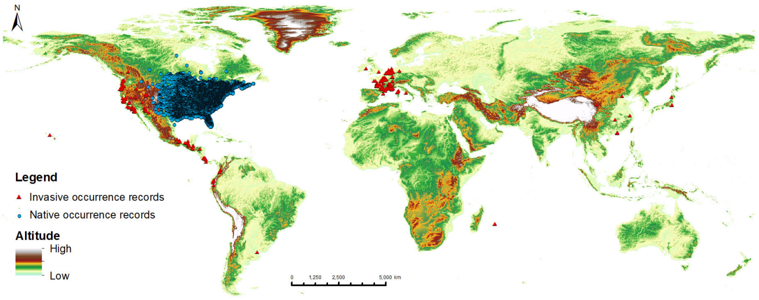

FIGURE 1
Map of global distribution of *C. serpentina*.

data. For future predictions, the Beijing Climate Center Climate System Model (BCC-CSM1-1) was employed, as it is widely utilized in the Asian region, and our primary focus is on species invasion issues in China (Dakhil et al., 2021). We selected climate and land cover variables for four "Representative Concentration Pathways" (RCPs: 2.6, 4.5, 6.0, and 8.5) for 2050 and 2070. The four RCPs represent hypothetical future greenhouse gas concentrations, ranging from low to high (van Vuuren et al., 2011). All environmental data were obtained at a high resolution of 2.5 arcminutes (equivalent to 5 km × 5 km). To avoid collinearity in our statistical models, we used Pearson's rank correlation coefficient to identify and remove highly correlated climate variables ($|r| > 0.70$) (Dormann et al., 2013). The final environmental variables incorporated into the model and subsequent analysis were Annual Mean Temperature, Mean Diurnal Range, Mean Temperature of Wettest Quarter, Annual Precipitation, Precipitation Seasonality, Precipitation of Warmest Quarter, Elevation, Water Bodies and Distance from Water Bodies.

2.2 MaxEnt model

Maximum Entropy Modeling (MaxEnt) is a useful method to simulate the potential habitat redistribution under climate change, due to high predictive accuracy and strong stability (Phillips et al., 2006; Wisz et al., 2008; West et al., 2016). Parameter optimization is critical for rigorously developing the model, as its purpose is to determine the optimal parameter combination that best represents the phenomenon of interest through finding the best fit to the data (Steele and Werndl, 2013; Jayasinghe and Kumar, 2019). We utilized the R 4.3.0 program and the kuenm package (Cobos et al., 2019) to evaluate candidate solutions on a global scale, encompassing all 31 possible combinations of the feature types (linear = l, quadratic = q, product = p, threshold = t, and hinge = h), and 10 regularization multiplier settings (0.1, 0.3, 0.6, 0.9, 1, 2, 3, 4, 5, and 6). The selection of optimal parameters for modeling hinged on three criteria: statistical significance, predictive power, and model complexity. The Partial ROC method was employed to gauge statistical significance (Peterson et al., 2008). Model performance was appraised via the omission rate (Anderson et al., 2003), whereas model complexity was ascertained by the AICc value (Warren et al., 2010). Previous research has shown that the model with the lowest AICc value (delta AICc = 0) is considered the best (Cobos et al., 2019). The final MaxEnt model's feature and regularization multiplier were selected based on the optimization process outcomes. The maximum number of background points was set to 10,000. For calibration, 70% of the occurrence records were utilized, with the remaining 30% used for model prediction evaluation. Extrapolation with clamping settings was applied, treating environmental conditions not encountered during model training as if they were at the limits of the training range. This approach holds fitted species responses at constant probabilities outside of training conditions, thereby limiting model extrapolations when projecting into novel environments (Elith et al., 2011). To ensure stable model predictions, the analysis included 10 replicate runs with cross-validation. Logistic regression was chosen as the output format, while all other parameters were set to the MaxEnt model defaults.

The predictive efficacy of the models was evaluated using the True Skill Statistic (TSS). Within the framework of species distribution models (SDMs), TSS is a threshold-dependent measure derived from sensitivity and specificity, or the probability that the model correctly predicts true presences and true absences, respectively (Allouche et al., 2006; Liu et al., 2009). TSS is extensively applied in assessing the predictions of SDMs. Interpretation of TSS values can be categorized as follows: values < 0.4 were poor, 0.4–0.8 useful, and > 0.8 good to excellent (Allouche et al., 2006). The impact of environmental variables on species distribution was assessed through percentage contribution (PC) analysis. PC is an intuitive and continuous measure of variable importance, was the most frequently reported metric (Bradie and Leung, 2017).

2.3 Classification of suitable habitats

We incorporated the results produced by MaxEnt software 3.3.4 (AMNH, New York, NY, USA) into ArcGIS 10.5 (ESRI, Redlands, CA, USA). The conversion tool was used to convert the data into raster data, and then the classification of suitable *C. serpentina* habitat was carried out using the reclassify tool. The comprehensive probability of suitable distribution regions was classified into four classes: unsuitable area ($0 \leq p \leq 0.1$), low-suitability area ($0.1 < p \leq 0.3$), medium-suitability area ($0.3 < p \leq 0.5$), and high-suitability area ($0.5 < p \leq 1$) (Yan et al., 2021).

2.4 Changes in suitable habitat area

We reclassified the MaxEnt output to a binary grid using the 10th training presence logistic threshold values (1 = above the threshold; 0 = below). The 10th training presence logistic threshold categorizes fewer than 10% of the training presence locations as unsuitable area (Capinha et al., 2013). To quantify the extent of changes in *C. serpentina* habitat distributions under future climate scenarios, we utilized the binary map and Python 2.7-based geographic information system (GIS) toolkits SDMtoolbox 2.5 (Brown et al., 2017). We calculated the change in suitable habitat for *C. serpentina* in China from the present to the future. The focus is on the central, eastern and southeastern regions, as well as 19 provincial administrative regions that currently have or will have suitable habitats in the future.

3 Results

3.1 Parameter selection and model evaluation

From an initial pool of 310 candidate models, only one set of model parameters met our selection criteria. In this candidate model (regularization multiplier = 1, feature class combination = lq), the mean AUC ratio was 1.686, the partial ROC was 0, the omission rate was 0.047, and the AICc was 149045.283. The average TSS value for 10 repeated runs is 0.76 (SD = 0.002), indicating that the MaxEnt model output based on model parameters can accurately simulate the potential distribution of *C. serpentina*.

3.2 Predicted habitat area of *C. serpentina* in the current climate

On a global scale, our results showed that optimal habitats for *C. serpentina*, apart from their indigenous regions, are predominantly located in western North America, southeastern and southern South America, southern Europe, a small range of northern central and southern Africa, eastern Asia and southern of Australia and New Zealand in Oceania. (Figure 2A). In China, high and middle suitable habitats are mainly distributed in the central and eastern regions, and there are scattered low suitable habitats in the southeast region (Figure 2B). Currently, the suitable habitat for *C. serpentina* in China only accounts for 4.34% of the total area (Figure 3). However, in the specific regions we are focusing on, the proportion of suitable habitat reaches 15.05% (Figure 4). Shanghai (91.74%), Anhui (58.69%), Hubei (56.73%), Henan (47.90%) and Jiangsu (42.72%) provinces face the highest risk of *C. serpentina* invasion, then followed by Jiangxi (23.35%), Zhejiang (18.09%) and Fujian (14.77%) provinces (Table 1). The most important environmental factors affecting the distribution of *C. serpentina* were Annual Precipitation (31.5%) and Annual Mean Temperature (27.5%), then followed by Precipitation Seasonality (17.6%) and Mean Diurnal Range (11.0%). The other five environmental factors had little effect on *C. serpentina* distribution (Table 2).

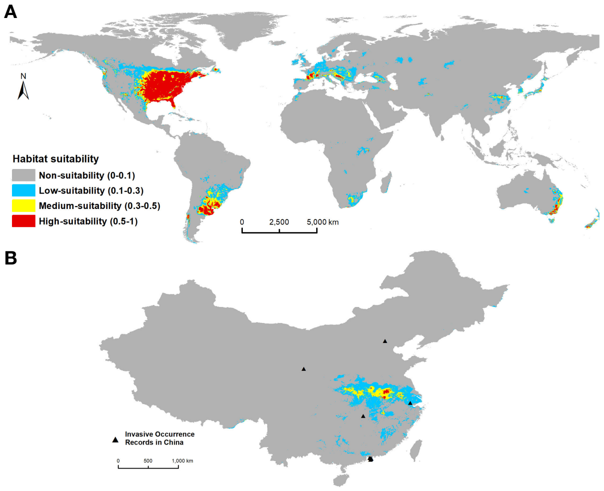

FIGURE 2
Under current climate conditions, the potential distribution area of *C. serpentina* in the world **(A)** and China **(B)**.

3.3 Effects of climate change on the habitat area of *C. serpentina* in China

Under various future climatic conditions, the potential geographic distribution range for the four climate change scenarios demonstrates a significant outward expansion. Within China, the future suitable habitat of *C. serpentina* is projected to expand by 30% to 90%, with new suitable habitat emerging in northeast China (Supplementary Figure 1). In the central, eastern, and southeastern regions of China that are the focus of our study, the changes in the area of suitable habitat align with the national scale changes. The suitable habitats in the central and eastern regions exhibit varying degrees of expansion, while there is some contraction in the southeast. In the RCPs2.6 and 4.5 scenarios, the suitable habitat in 2070 is expected to decrease to some extent compared to 2050, whereas the RCPs6.0 and 8.5 scenarios show an increase (Figure 4). Among the eight provinces with more than 10% suitable habitat, only Fujian Province is projected to experience a downward trend in the future, while the remaining seven provinces

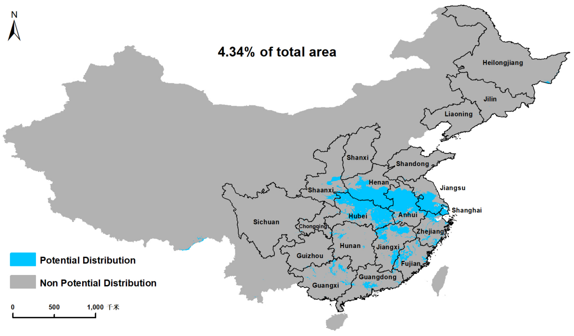

FIGURE 3
Under current climatic conditions, the binary map of potential distribution area of *C. serpentina* in China.

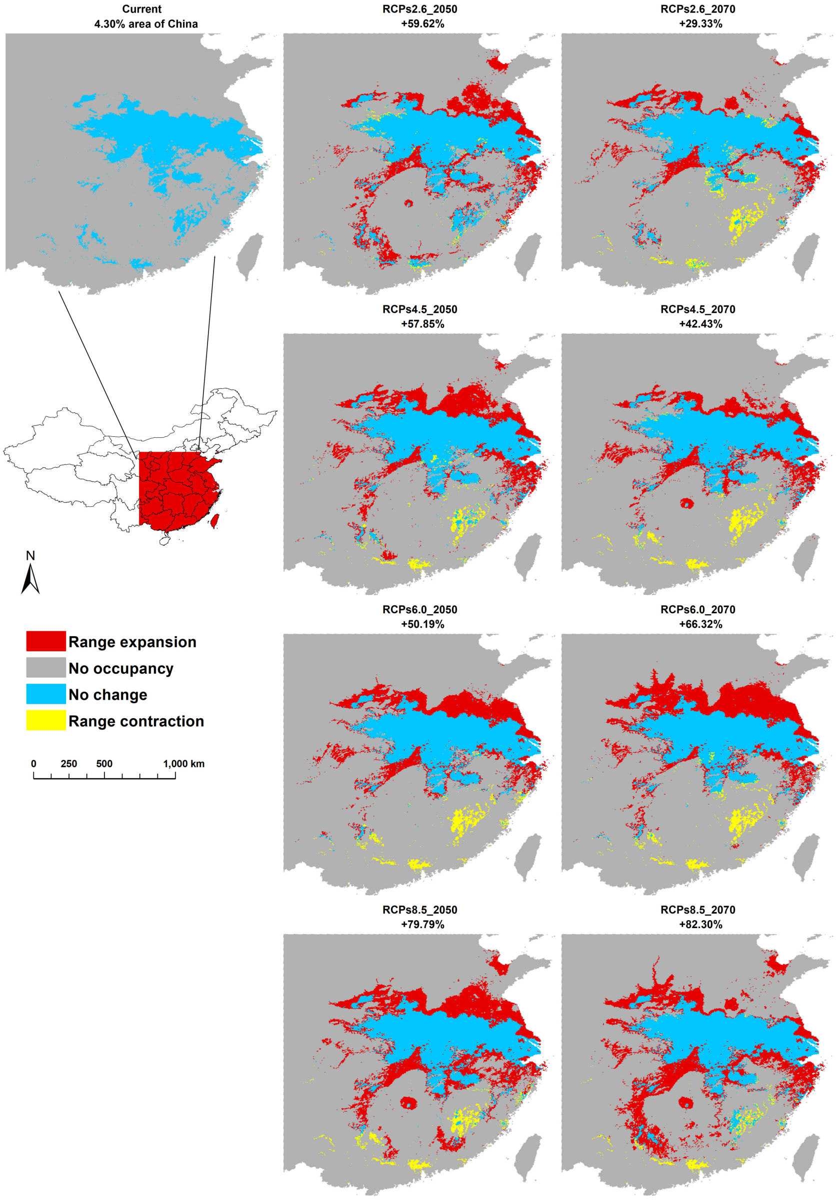

FIGURE 4
The changes in the potential distribution of *C. serpentina* in central, eastern, and southeastern China from the current conditions to 2070 under the climate scenarios of RCP2.6, RCP4.5, RCP6.0, and RCP8.5.

are expected to see an upward trend, particularly Jiangsu and Zhejiang Province, which may experience two to three times growth. Among the twelve provinces where the current proportion of suitable habitats is less than 10%, Guangdong and Guangxi will show a downward trend in some scenarios, while the remaining ten provinces will show an upward trend, especially Shaanxi and Hunan provinces, where the proportion of suitable habitats may exceed 20% in the future (Tables 1, 3).

4 Discussion

Risk maps play a crucial role in the strategic management of IAS by visually displaying potential settlement areas. The research findings indicate that, given current climate conditions, the potential invasion range of *C. serpentina* in China is relatively low. But the central, eastern, and southeastern regions of China that we are focusing on have a high risk of invasion currently and in the future. Presently, Shanghai, Anhui, Hubei, Henan, and Jiangsu provinces face a high risk of invasion, while Jiangxi, Zhejiang, and Fujian provinces have a relatively low risk. Existing research reports indicate that only the Hong Kong region in China has recorded dense wild sightings of *C. serpentina* (Sung et al., 2021). However, Hong Kong does not fall within the suitable habitat range according to our findings. Therefore, we believe that the individuals found in the region were more likely released into the wild during the captive breeding period, though this requires further field investigation. Through online information retrieval, we

TABLE 1 Share of current and 2050 C. *serpentina* habitat areas in 20 provincial administrative regions.

Province	Total area (km^2)	Current	RCPs2.6	RCPs4.5	RCPs6.0	RCPs8.5
Shanghai	6,300	91.74%	99.17% ↑	100% ↑	97.52% ↑	98.35% ↑
Anhui	139,700	58.69%	70.05% ↑	76.68% ↑	76.17% ↑	86.24% ↑
Hubei	185,900	56.73%	68.83% ↑	67.27% ↑	70.46% ↑	75.71% ↑
Henan	167,000	47.90%	60.81% ↑	77.53% ↑	75.09% ↑	77.55% ↑
Jiangsu	102,600	42.72%	87.36% ↑	85.75% ↑	95.79% ↑	94.74% ↑
Jiangxi	167,000	23.35%	35.35% ↑	21.98% ↓	23.16% ↓	36.15% ↑
Zhejiang	102,000	18.09%	48.05% ↑	60.64% ↑	44.14% ↑	54.15% ↑
Fujian	121,300	14.77%	21.09% ↑	7.56% ↓	0.57% ↓	8.68% ↓
Shaanxi	205,600	7.04%	9.00% ↑	15.07% ↑	16.95% ↑	19.80% ↑
Guangdong	180,000	5.75%	9.78% ↑	1.24% ↓	0% ↓	5.92% ↑
Guangxi	236,000	5.37%	15.83% ↑	6.76% ↑	2.71% ↓	3.95% ↓
Hunan	211,800	2.35%	13.66% ↑	12.00% ↑	11.00% ↑	21.96% ↑
Chongqing	82,300	0.88%	5.77% ↑	11.96% ↑	14.8% ↑	7.18% ↑
Guizhou	176,000	0.34%	2.63% ↑	2.63% ↑	1.82% ↑	3.77% ↑
Heilongjiang	473,000	0.24%	1.51% ↑	3.38% ↑	2.36% ↑	2.62% ↑
Shanxi	156,300	0.14%	1.45% ↑	4.02% ↑	5.60% ↑	5.90% ↑
Shandong	153,800	0.12%	15.94% ↑	17.25% ↑	6.11% ↑	20.94% ↑
Jilin	184,700	0.04%	10.46% ↑	0.12% ↑	0.17% ↑	3.45% ↑
Liaoning	145,900	0.02%	5.49% ↑	0.01% ↓	0.21% ↑	0.57% ↑
Sichan	481,400	0.02%	0.34% ↑	0.96% ↑	1.44% ↑	0.71% ↑

"↑" indicates an increase in *Chelydra serpentina* habitat share, while "↓" indicates a decrease.

discovered news reports indicating the presence of *C. serpentina* in the wild environment across all eight provinces that face a high risk of invasion. *C. serpentina* has been discovered in China for over a decade (Liu et al., 2021), but the status of its invasion in the country remains entirely unknown. It is imperative that China conducts an urgent investigation into the status of *C. serpentina* invasion.

TABLE 2 Average percentage contribution (PC) of environmental variables in MaxEnt for *C. serpentina*.

Environmental variable	PC (%)
Annual Precipitation	31.5
Annual Mean Temperature	27.5
Precipitation Seasonality	17.6
Mean Diurnal Range	11.0
Precipitation of Warmest Quarter	5.2
Distance from Water Bodies	4.2
Elevation	2.1
Mean Temperature of Wettest Quarter	0.8
Water Bodies	0

Annual precipitation and annual mean temperature are the most significant variables limiting the suitable habitat of the *C. serpentina*. Established populations of *C. serpentina* are most frequently occur in ponds, marshes, swamps, peat bogs, shallow bays, river and lake edges, and slow-moving streams (Harding and Mifsud, 1997; Ernst and Lovich, 2009; Paterson et al., 2012). The dependence on water bodies makes annual precipitation the most important factor in predicting the distribution of *C. serpentina*. Although *C. serpentina* can hibernate in soil (Brown and Brooks, 1994), or raise their body temperature by sunning their backs (Obbard and Brooks, 1979), their eggs require a hatching temperature of above 20°C to survive, and the appropriate hatching temperature can increase the survival rate of *C. serpentina* hatchlings (McKnight and Gutzke, 1993; O'Steen, 1998; Rollinson et al., 2012). Consequently, the average annual temperature is also important for the distribution of *C. serpentina*. The lack of effect of water bodies and distance from water bodies on the distribution of *C. serpentina* may be due to their extensive nesting and terrestrial migration in wetlands within their range to cope with extreme conditions such as drought (Steen et al., 2010), leading to a lower dependency on water bodies. Another explanation lies in the fact that climate variables can directly provide mechanisms and physiological explanations for species distribution, but land cover are supposed to have little direct

TABLE 3 Share of current and 2070 *C. serpentina* habitat areas in 20 provincial administrative regions.

Province	Total area (km^2)	Current	RCPs2.6	RCPs4.5	RCPs6.0	RCPs8.5
Shanghai	6,300	91.74%	100% ↑	99.72% ↑	97.80% ↑	100% ↑
Anhui	139,700	58.69%	64.79% ↑	77.18% ↑	80.57% ↑	77.73% ↑
Hubei	185,900	56.73%	68.83% ↑	71.98% ↑	68.25% ↑	76.55% ↑
Henan	167,000	47.9%	65.48% ↑	66.15% ↑	85.32% ↑	71.04% ↑
Jiangsu	102,600	42.72%	58.12% ↑	77.45% ↑	99.16% ↑	60.50% ↑
Jiangxi	167,000	23.35%	15.35% ↓	23.75% ↑	17.61% ↓	35.87% ↑
Zhejiang	102,000	18.09%	44.87% ↑	56.49% ↑	49.25% ↑	63.33% ↑
Fujian	121,300	14.77%	3.07% ↓	1.94% ↓	1.71% ↓	6.31% ↓
Shaanxi	205,600	7.04%	16.89% ↑	11.62% ↑	26.37% ↑	24.05% ↑
Guangdong	180,000	5.75%	0.95% ↓	0% ↓	0.74% ↓	4.88% ↓
Guangxi	236,000	5.37%	6.50% ↑	1.35% ↓	2.98% ↓	16.91% ↑
Hunan	211,800	2.35%	8.16% ↑	12.25% ↑	8.32% ↑	28.91% ↑
Chongqing	82,300	0.88%	10.36% ↑	15.77% ↑	10.63% ↑	14.68% ↑
Guizhou	176,000	0.34%	1.13% ↑	1.82% ↑	2.65% ↑	10.08% ↑
Heilongjiang	473,000	0.24%	1.55% ↑	4.74% ↑	6.57% ↑	2.49% ↑
Shanxi	156,300	0.14%	3.61% ↑	2.99% ↑	13.81% ↑	9.93% ↑
Shandong	153,800	0.12%	2.95% ↑	2.58% ↑	22.62% ↑	10.04% ↑
Jilin	184,700	0.04%	0.29% ↑	5.79% ↑	4.08% ↑	5.09% ↑
Liaoning	145,900	0.02%	0.08% ↑	0.57% ↑	0.19% ↑	9.98% ↑
Sichan	481,400	0.02%	1.23% ↑	1.44% ↑	0.99% ↑	1.08% ↑

"↑" indicates an increase in *Chelydra serpentina* habitat share, while "↓" indicates a decrease.

physiological relevance for species (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003). Because land cover can only be applied within limited geographical ranges without significant errors, as the same land cover type can correspond to different climate combinations in different regions or time periods (Guisan and Zimmermann, 2000). Hence, the distribution of a species at the continental scale primarily depends on its climate tolerance rather than the type of land cover (Pearson and Dawson, 2003; Thuiller et al., 2004).

Climate change is expected to cause the expansion of suitable habitats in all scenarios. The suitable habitat shows a pattern of significant initial increase with the intensity of climate change, followed by a slight decrease, and ultimately increasing again. The central and eastern regions' suitable habitats will significantly expand toward the north and south. Among the eight provinces currently facing higher risk, except for Fujian Province, the other seven provinces will indeed face even more severe invasion risks in the future. The suitable habitats in Shaanxi and Hunan provinces may account for more than 20% in the future. We strongly recommend the establishment of long-term monitoring plans for *C. serpentina* in Shaanxi, Hunan, and the eight provinces currently facing higher risk.

Turtles, symbolizing luck and longevity in Chinese culture, are popular as pets and extensively used for food and traditional medicine (Cheung and Dudgeon, 2006; Zhou and Jiang, 2008). The turtle farming industry in China has seen rapid expansion since the 1990s to meet this significant demand (Wu et al., 2020). Freshwater turtles, especially favored in the pet trade, are frequently abandoned by their owners or intentionally released into the wild during religious events, potentially leading to their establishment in new habitats (Perry et al., 2007; Masin et al., 2014). Despite being a relatively species-poor order, turtles have been introduced more frequently than any other reptiles (Kraus, 2009). The worldwide pet trade has documented at least 61 species of chelonians (Gong et al., 2009). In the Chinese turtle trade market, alien species constitute approximately 67.05% (Hong et al., 2022). As per 2023 data, 43 species of the order Testudines inhabit China, including 39 native and 4 invasive alien species (Ji, 2023). China's rapidly developing e-commerce industry is facilitating the purchase and release of potential invasive turtle species within the country (Liu et al., 2021). Among the eight provinces currently facing higher risk of invasion, except for Jiangxi Province, the Gross Domestic Product (GDP) of the other seven provinces ranks within the top ten in China, and their developed economy will further promote the establishment of IAS (Gallardo, 2014). Moreover, turtle farms are heavily concentrated in the provinces of Zhejiang, Jiangsu, and Guangdong within these regions (Zhou and Huang, 2007), which heightens the risk of species escaping. The existence of irrigation channels could further aid the dispersal of this specie to more remote areas (Alles et al., 2022). In conclusion, human activities are likely to increase the chances of *C. serpentina* establishing stable populations in their suitable habitats.

According to the Convention on Biological Diversity, which establishes a “three-stage hierarchical approach,” priority should be given to prevention in high-suitability areas where the species has not yet been recorded (UNEP Mittermeier, 2002). Given the limited knowledge we currently have about the extent of *C. serpentina* invasion in China, it is essential to prioritize monitoring efforts in the areas indicated by our risk map. Citizen science, which involves public participation in data collection and analysis, has proven to be an effective approach for monitoring biological invasions and detecting IAS at an early stage (Kalaentzis et al., 2023). Although the unique shape traits of *C. serpentina* make it easier to identify in the wild (Ernst and Lovich, 2009), underwater observation can still be challenging. A solution to this challenge is the use of environmental DNA (eDNA) technology, which detects genetic material from the organisms’ surroundings (Kelly et al., 2014). By combining citizen science engagement with a simple eDNA sampling toolkit, public awareness of invasive organisms such as *C. serpentina* can be increased, and the efficiency of scientific monitoring can be greatly improved (Zhang et al., 2023). Using trained dogs to detect *C. serpentina* through olfaction would be an efficient investigation method (Kapfer et al., 2012). During May-August of the year and in the morning and afternoon of the day, *C. serpentina* is the most active period and the best time to investigate (Obbard and Brooks, 1981). The primary area of investigation is the surrounding vicinity of a permanent body of water (Graves and Anderson, 1987).

For government agencies, effectively managing invasive species from a legal and enforcement perspective is crucial. In America, *C. serpentina* lacks endangered species classification yet faces significant threat from unprecedented harvesting meeting international market demands. In response to the over-commercial harvest and the resulting decline in *C. serpentina* populations, certain states in the United States have already taken steps to ban this practice (Colteaux and Johnson, 2017). *C. serpentina* was listed in the Appendix II of the Washington Convention (CITES, Convention on International Trade in Endangered Species) in 2023. The illegal possession and trafficking of these animals will be punished under the Chinese Wildlife Protection Law. However, the specific implementation of the law is still being explored, especially given the challenges posed by China’s large market for this species.

The reliability of extrapolating SDMs to new ranges and future climates has been extensively debated (Sequeira et al., 2018). One important factor influencing the model’s ability to extrapolate is the number of occurrences used in model calibration. In our study, we utilized 7,897 occurrence data for model calibration. This abundance of occurrence data helps mitigate the influence of outliers during model calibration (Guisan and Thuiller, 2005). We studied a species that has a very wide distribution in North America, and the wide range and many native occurrence data mean that *C. serpentina* live in a wider range of climates, resulting in a relatively large native niche and a more conservative niche than specialist species (Li et al., 2014; Liu et al., 2020). The conservatism of the climate niche in *C. serpentina* enhances the reliability of our results when extrapolating the calibrated model to new ranges (Liu et al., 2020). Despite the limitations of SDMs (Pearson and Dawson, 2003; Record et al., 2018), this method remains one of the most promising tools for predicting the potential distribution of invasive species (Bellard et al., 2013; Hill et al., 2017), which is a fundamental objective of conservation biology (Jeschke and Strayer, 2008).

In addition to the controversy over model extrapolation, there are some limitations to our simulation results. We did not consider source populations, biotic interactions, and the dispersal capacity and pathway of *C. serpentina*. The species has multiple geographic lineages within its native rang (Iverson et al., 1997; Ewert et al., 2005), and if the environmental tolerances of these geographic lineages differ, the introduced population may only occupy a portion of the entire niche (Jeschke and Strayer, 2008; Tingley et al., 2016). As we do not know which geographic lineages were introduced to China, we may have overestimated the suitable habitat for *C. serpentina* in China. Biotic interactions, such as competition and predation, directly influence the distribution of species at a local scale (Jeschke and Strayer, 2008; Yates et al., 2018). Our results can only be interpreted as suitable habitats under abiotic environmental factors. The dispersal capacity and pathway of invasive species significantly affect the scope and speed of invasion (Hulme, 2009). As *C. serpentina* has weak dispersal abilities (Obbard and Brooks, 1981), releasing them into the wild is likely the primary way they spread in China (Liu et al., 2021; Sung et al., 2021). Therefore, it is crucial to consider local customs and habits when investigating their distribution. The occurrence data we used on a global scale comes from the GBIF database, which has spatial bias that is challenging to eliminate, even when carrying out spatial sparsity processing (Beck et al., 2014). Furthermore, there are several inherent limitations to using presence-only data (Yackulic et al., 2013).

5 Conclusion

Our modeling indicates that suitable habitats for *C. serpentina* are currently concentrated in central, eastern, and southeastern China, with Shanghai, Anhui, Hubei, Henan and Jiangsu provinces facing the highest risk of invasion. Climate change may substantially expand future suitable areas, and multiple provinces will face a more severe threat of invasion. To prevent the establishment and spread of *C. serpentina*, we urgently recommend implementing monitoring programs that leverage the integration of citizen science, eDNA technology, and other methods, particularly in high-risk regions. Moreover, the government should address legal and enforcement challenges associated with the trade of this species. While our modeling has some inherent limitations, it nonetheless offers valuable scientific support for managing *C. serpentina* invasion in China. Further research incorporating source populations, biotic interactions and dispersal abilities would provide greater insight into the invasion dynamics of this generalist turtle species. Actively preventing and early detecting *C. serpentina* is of paramount importance for the conservation of China’s freshwater ecosystems.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.15468/dl.rvmyvk.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because, although we conducted research on vertebrates, we only obtained occurrence data and analyzed it through databases. We did not conduct animal experiments nor had direct contact with animals.

Author contributions

CM: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. PL: Conceptualization, Funding acquisition, Project administration, Supervision, 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.2023.1277058/full#supplementary-material

SUPPLEMENTARY FIGURE 1
Changes in the potential distribution of *C. serpentina* in China from the current conditions to the 2070 under the climate scenarios of RCP2.6, RCP4.5, RCP6.0, and RCP8.5.

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Short-term influences of flow alteration on microbial community structure and putative metabolic functions in gravel bar hyporheic zones

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Microbial communities in the hyporheic zone are important for self-purification as the riverbed is metabolically active and responsible for the retention, storage, and mineralisation of organic matter transported in the surface water. Studies exploring the response of the hyporheic microbial community to flow regime alterations remain scarce. Here, we characterised the microbial community structure over downwelling, upwelling and intermediate hyporheic zone areas within and among gravel bars at high and low discharge levels to determine flow-induced changes in a dam-regulated river using 16S rRNA gene sequencing. At low discharge, microbial composition varied across the different areas of gravel bars, reflecting heterogeneity in local abiotic conditions. However, high discharge lead to microbial community homogenisation across the three areas of the gravel bars. Microbial communities across adjacent gravel bars remained dissimilar regardless of discharge levels, likely reflecting differences in bar morphology. Our results can help better understand how anthropogenic changes in hydrologic conditions can affect microbial diversity and function in the hyporheic zone. This knowledge will help us to understand better how changes in hydrological conditions affect ecosystem functions and services in rivers affected by human impacts.

KEYWORDS

hyporheic zone, microbial community structure, 16S rRNA gene sequencing, river discharge, putative metabolic function

Introduction

Rivers are dynamic environments and examining how flooding affects community structure has long been an important research topic in disturbance ecology (Graham et al., 2021). However, previous studies focused only on surface water organisms such as microbiota, fishes, and macroinvertebrates (Dole-Olivier et al., 1997; Calderon et al., 2017; Miyake et al., 2021). Limited studies were done on organisms in the hyporheic zone. In riverine ecosystems, the hyporheic zone in gravel bars is essential in providing habitat and refuge for microbial communities (Boulton and Stanley, 1995; Boulton et al., 2010; Boano et al., 2014; Harjung et al., 2019) and in maintaining healthy waterways

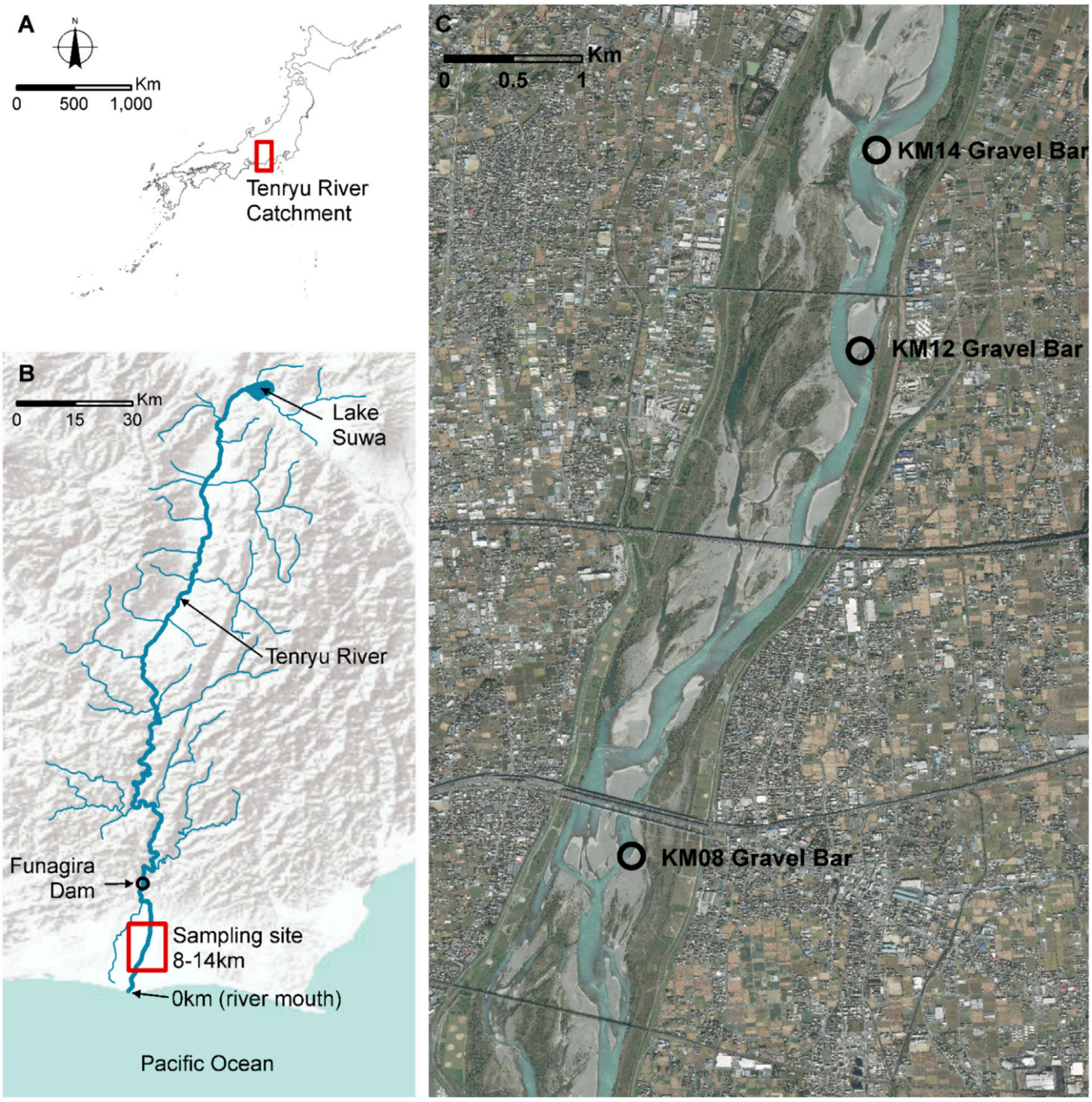

FIGURE 1
Detailed map of the sampling sites **(A)** The top panel shows the contour of the map of Japan indicating the Tenryu River. **(B)** The figure shows the location of Lake Suwa where the river originates and Funagira Dam over Esri elevation model. **(C)** Google map aerial photo of the three gravel bars (KM08, KM12 and KM14) from the river mouth.

(Lewandowski et al., 2019). This hyporheic flow carries different materials with it and other microbial communities, removing water pollutants and natural solutes.

In the hyporheic zone, environmental conditions can vary widely between areas of downwelling zone (surface water movement toward the groundwater) at the bar head to the upwelling zone (groundwater movement toward the surface water) at the bar tail of the gravel bar water flows into the hyporheic zone (Hendricks, 1993). Increased discharge in a river, i.e., dam-regulated discharge, can increase hydraulic pressure on the riverbed, potentially increasing the downwelling flow from the surface water to the hyporheic zone, or the flow velocity of the normally slow-flowing hyporheic water. Such changes in the hydrologic conditions could result in hyporheic zone community disturbance during flooding. If a heterogeneous community structure is formed along the hyporheic zone path of gravel bar under low discharge conditions, a disturbance occurring under high river surface water discharge, such as a flood, could homogenise microbial communities. To test this hypothesis, the composition and community structure of microbial communities should be compared within and across gravel bars, during periods of contrasting streamflow levels. Limited studies focused on the effects of low regulation on microbial diversity in the hyporheic zone. One study focused on the altered flow regime as disturbance ecology (Bruno, et al., 2023). However, this study did not focus on differences in microbial community structure across different areas of hyporheic gravel bars.

Previous studies used molecular approaches to investigate how the hyporheic flow path influences microbial communities in hyporheic zones in gravel bars (Doering et al., 2021). For example, one study

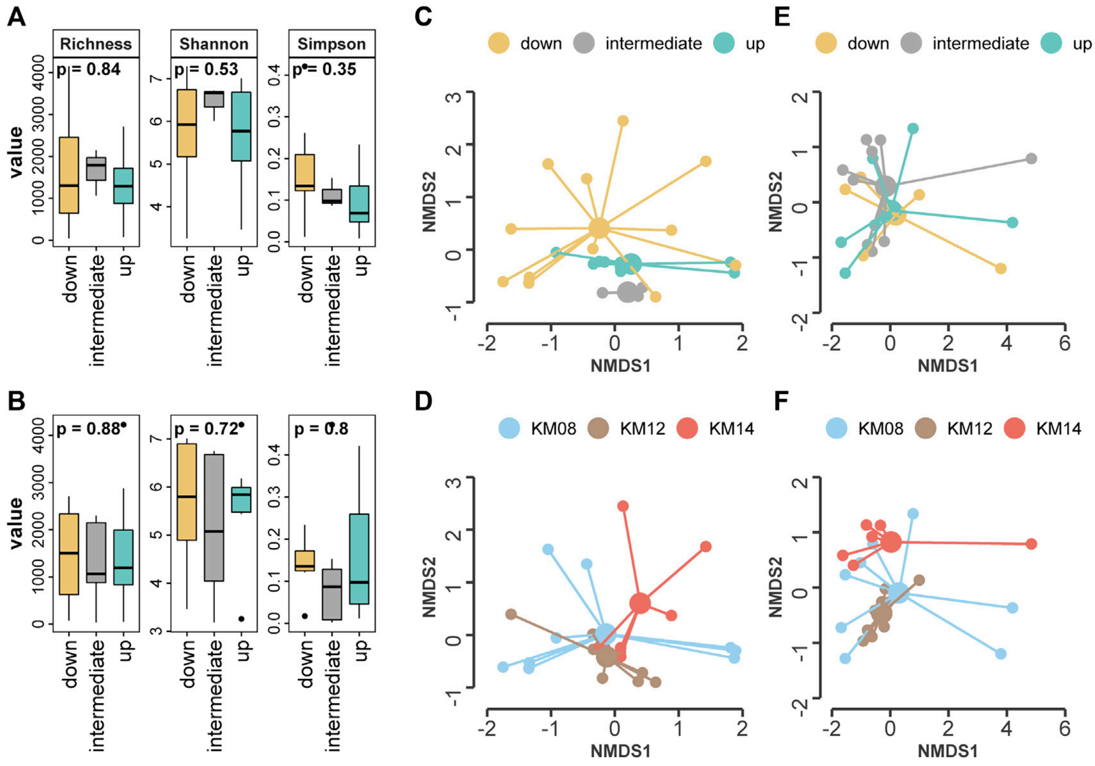

FIGURE 2
Non-multidimensional scaling (NMDS) showing the microbial community structure in **(A)** low discharge by hyporheic area **(B)** low discharge by gravel bar **(C)** high discharge by hyporheic area **(D)** high discharge by gravel bar. Box plot showing the alpha diversity per hyporheic area (i.e., downwelling, upwelling and intermediate) **(E)** Alpha diversity in low discharge **(F)** Alpha diversity in high discharge.

TABLE 1 Distance-based redundancy (dbRDA) analysis shows the environmental factors affecting the microbial community structure for each gravel bar in two discharges levels.

Discharge	Physico-chemical characteristics	*p*-value
Low	Turbidity	0.002
	EC	0.001
	Al	0.019
High	pH	0.033
	Ca	0.011

demonstrated microbial communities were spatially diverse along a 100-m hyporheic flow path with large environmental heterogeneity such as chemicals and nutrients using polymerase chain reaction-denaturing gel electrophoresis (PCR-DGGE) (Lowell et al., 2009). One study how vertical flow direction (i.e., upwelling/downwelling) affect the microbial community and identified different microbial community compositions between the upwelling/downwelling zones using pyrosequencing (Kim and Lee, 2019). Our study focused on microbial community diversity in response to altered flow disturbance in different areas of hyporheic zone in gravel bars using 16S rRNA gene sequencing.

Understanding the functional traits of each species could contribute to deepening our knowledge of the biological processes and ecological mechanisms that shape community structure variation along environmental gradients. Recent studies on freshwater microbial communities also estimated functional traits based on taxonomic annotation using databases (e.g., SILVA rRNA, Greengenes, National Center for Biotechnology, and Ribosomal Database Project) and 16S rRNA gene sequencing (Galand et al., 2018; Fasching et al., 2020; Serrana et al., 2022). Several studies have demonstrated the validity and utility of this approach, although the estimated functional traits were putative as 16S rRNA gene sequencing could not identify functional genes in the genome, and database limitations allowed annotating only a proportion of the taxa. However, applied cases are still scarce and further verifications would be required.

Our study examined the effects of flow regulation as a disturbance for the hyporheic microorganisms. In particular, we aimed to 1) profile the microbial diversity and community structure among hyporheic zones at three hyporheic, i.e., downwelling, upwelling, and intermediate, areas of gravel bars, 2) identify the microbial community structure-influencing environmental factors among the hyporheic zones areas, 3) compare the divergence levels of the microbial communities among the hyporheic areas under low and high discharge conditions of the river surface water, and 4) identify the putative metabolic functions of the microbial communities on these sites under different discharge levels. This study can provide valuable insights into the role of spatial environmental heterogeneity in the biological processes and ecological mechanisms that govern the local adaptation of

TABLE 2 PERMANOVA of the three points in low and high discharge.

Discharge	Df	SumsofSqs	MeanSqs	F Model	R2	Pr(>F)
Low	2	1.1201	0.56006	2.0685	0.16458	0.004
High	2	0.6663	0.33314	1.0589	0.09575	0.326

microbial communities at taxonomic and functional levels in gravel bar hyporheic zones.

Materials and methods

Study site and water sample collection

The Tenryu River is located in central Honshu, Japan, with a length and basin area of 213 km and 5,090 km^2, respectively. The river originates from Lake Suwa in Nagano Prefecture and is discharged into the Pacific Ocean (Figure 1). The Funagira Dam (34°53′26′N, 137°48′54′) is the last major dam to be completed on the Tenryu River supplying water to the nearby Funagira Hydroelectric Power Station. The dam releases different water discharge levels throughout the year, thereby altering the water flow discharge of the river.

Visual inspection of sampling sites was done before the actual field survey. Field surveys were conducted between November 13–17, 2019. The mean dam discharge was high (250 m^3/s) and low (150 m^3/s) between November 13–15 and 16–17, 2019, respectively. During the field survey, flow fluctuations reduced the water level to 80 cm, thereby changing gravel bar morphology. Three gravel bars located 8, 12, and 14 km (KM08, KM12 and KM14, respectively) from the river mouth were selected in this study. These three large gravel bars are distributed adjacent to each other within 6 km of the middle reach of the Tenryu River, with relatively similar environmental conditions. We collected and measured water samples and environmental parameters at three sampling areas among each gravel bar site. The downwelling area can be defined as the area at the upper side of gravel bar where surface water enters the hyporheic zone, the upwelling area can be defined as the area at the lower side of gravel bar where hyporheic water upwells. The intermediate area is located on the between the down area and the up area.

However, no sample was collected from the intermediate area of gravel bar KM14 as no hyporheic water was collected 20 cm from the ground. In total, we assessed 16 sampling areas, $n = 8$ both at low and high discharges, in this study and collected water samples in triplicates for each sampling area (a total of 48 water samples).

A 1,220-mm-long solid steel cone piezometer (AXEL, Japan) was used to collect water samples from a depth of 20 cm from the ground surface at each hyporheic area. Hyporheic water samples of 250–500 mL was filtered using a 50-mL sterile syringe (Terumo) and 0.22-µm Sterivex™ filters (Merck Millipore, Merck KgaA, Darmstadt, 346 Germany) on-site. A negative field control sample was produced by filtering 1 L of ddH2O through a Sterivex™ filter, similar to the field samples. The filtered samples were preserved in 99% molecular-grade ethanol, brought to the laboratory, and stored at −20°C until processing for molecular analysis.

Water quality parameters, i.e., pH, electrical conductivity (EC), water temperature and turbidity, were recorded *in situ*. pH, EC, and water temperature were measured with a multi-parameter water quality checker (HORIBA, D-54, Japan). Turbidity was measured with a portable turbidity metre (TB-31, DKK-TOA, Japan). Suspended solids (SS) were collected by filtering 0.5 litres of hyporheic river water, passing it through a 1-mm sieve onto a GF/F filter (pore size: 0.7 µm), drying (105°C, 4°h) and weighing on an electronic balance. Anions (F-, Cl-, NO_3-N, $SO_4$2-) were measured using ion chromatography (Metrohm, Basic IC plus 883, Swiss). Inorganic elements (Mg, Al, and Na) were measured using an inductively coupled plasma mass spectrometer (Agilent Technologies, Agilent8800 ICP-QQQ, Japan).

DNA extraction, library preparation and amplicon sequencing

Total genomic DNA was extracted from each filter using the Qiagen PowerSoil DNA Isolation Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. DNA quality and concentration were determined using a NanoDrop spectrophotometer (Thermo Scientific Nanodrop 2,000), and the QuantiFluor dsDNA System (Promega, Madison, United States). The amplicon library was prepared through a one-step PCR protocol using modified primer sequences targeting the V4-V5 hypervariable region of the 16S SSU rRNA gene from the Earth Microbiome Protocol (Caporaso, et al., 2012). The forward sequence is 515F AATGATACGGCGACCACCGAGATCTACACGCT and the reverse primer sequence was 926R CAAGCAGAAGACGGCATACGAGATAGTCAGCCAGGGCCGYCAATTYMTTTRAGTTT. The PCR was performed using a T100 Thermal Cycler (Bio-Rad Laboratories, United States) and Phusion high-fidelity DNA polymerase (New England, Biolabs) for the PCR amplification. The 15-µL PCR reaction mixture consisted of 3 µL of 5X Phusion GC Buffer, 0.5 µL each of both the forward and reverse primers (10 µM), 0.6 µL dNTPs (2.5 mM), 0.45 µL DMSO, 0.3 µL Phusion Polymerase (1U), and 1 µL of template DNA at a concentration of 5 ng/µL. The PCR cycling conditions were as follows: initial denaturation at 98°C for 3 min, 25 cycles of denaturation, annealing, and extension at 98°C for 15 s, 67°C for 30 s, and 72°C for 30 s, respectively, followed by a final extension cycle at 72°C for 5 min. The amplicon size was 420 bp. Two negative controls, i.e., field control sample filtered from sterile water and nuclease-free water were included to monitor the potential contamination from DNA extraction to PCR amplification. A total of 50 amplicon libraries (i.e. 2 negative controls, and triplicates of 16 areas) were constructed. The PCR products were verified on a 2% agarose gel using gel electrophoresis. Next, we quantified the concentration of each PCR product using the KAPA

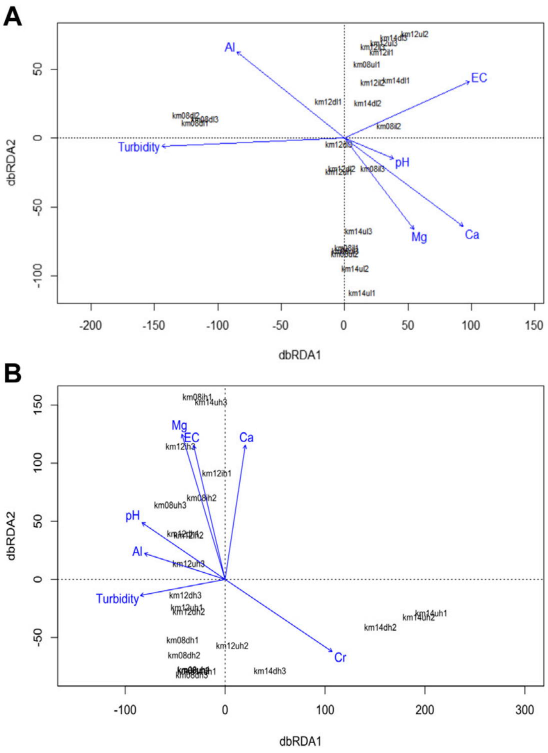

FIGURE 3
The dbRDA plot showing the significant environmental factors influencing microbial community: **(A)** dbRDA in low discharge **(B)** dbRDA in high discharge.

Illumina Library qPCR Quantification kit (Kapa Biosystems, Wilmington, MA, United States). Equimolar concentrations of each amplicon library were then pooled. The pooled samples were purified and size-selected using solid-phase reversible immobilisation beads (Beckman Coulter, Inc. CA). We used the Agilent Bioanalyzer 2100 system to assess the quality of the pooled library by the obtention of a single clear band of 420 bp. Sequencing was conducted on an Illumina Miseq (Illumina, Inc. San Diego, CA, United States) using a v3 Miseq sequencing kit (300 × 2, MS-102-3003) with 30% PhiX (Illumina, Inc. San Diego, CA, United States) and a starting concentration of 4 nM denatured to a final concentration of 8pm.

Read processing and taxonomic assignment

Raw paired-end reads were verified for quality using FastQC v0.11.8 (Andrews, 2010). The raw reads were demultiplexed using the QIIME v2018.11 package (Boylen et al., 2019). Demultiplexed sequence data were then quality screened, processed and denoised using the DADA2 pipeline v1.16 package (Callahan et al., 2016). The reads were quality-filtered and truncated into 100-bp fragments. The chimeric sequences and singletons were also removed. Based on the read error files, the reverse reads displayed poor read quality. Therefore, only the forward reads were processed for downstream analyses. Amplicon sequence variants (ASVs) were inferred from the sequence data using the DADA2 pipeline v1.16 package. Taxonomic ASV identification was performed against the SILVA SSU database v132 using the SILVA ACT (www.arb-silva.de/aligner) (Pruesse et al., 2012). Subsequent analyses were performed at the ASV-level.

Statistical analyses and visualisation

All statistical analyses and visualisations were performed using the R software v4.0.1 (R Core Team, 2018). Read number normalisations were performed in each sample using median sequencing depth before the analyses as an alternative to total counts because it is less influenced by most highly abundant taxa, while not disregarding rare taxa. Species diversity at each area (alpha diversity) was determined using Chao1 richness (Chao, 1984), Shannon diversity (Shannon, 1949), and Simpson diversity (Simpson, 1949) via the plot_richness command in the phyloseq package (McMurdie and Holmes, 2015). The mean alpha diversity values for each replicate in the hyporheic areas were computed. Analysis of variance (ANOVA) was conducted via phyloseq to test whether the mean alpha diversities were significantly different among the three or two areas per gravel bars. Differences in microbial composition among areas of the gravel bars were computed using Bray–Curtis dissimilarity (Bray and Curtis, 1957) in vegan package, and visualised by non-metric multidimensional scaling (NMDS) using the plot_ordination function in the phyloseq package (Dixon, 2003). Permutational multivariate analysis of variance (PERMANOVA) was measured using the phyloseq package to test potential significant differences between areas per gravel bars (Anderson et al., 2008). Distance-based redundancy analysis (dbRDA) was performed to determine the environmental factors influencing the microbial community structure among the hyporheic areas and visualised via the cca function of the vegan package. We identified the putative metabolic functions using the functional annotations for the prokaryotic (FAPROTAX) v1.2.3 (Louca et al., 2016; Louca and Doepeli, 2017) database. The mantel test (Legendre and Legendre, 2012) was conducted via the mantel.correlog function with 9.999 permutations to test for significant correlations between beta diversity based on taxonomic structure among the areas and that based on the putative metabolic function structure.

Results

Microbial diversity and community composition

We generated a total of 15,346,131 raw reads from the 50 amplicon libraries. The reads one and six of the two negative controls were removed for subsequent analyses. After quality filtering, chimeric sequence removal and denoising, we retained a total of 5,439,168 reads (Supplementary Table S1). Out of the inferred 19,592 ASVs, only 5,453 ASVs exhibited genus level, and from the latter, 260 ASVs species-level assignments. At the genus level, *Flavobacterium* (440,130 reads, 21% of the total number of reads assigned to genera) was the most abundant among the three different areas followed by *Methylobacter* (115,342 reads, 6%), *Sediminibacterium* (92,722 reads, 5%), and *Rhodoferax* (88,531 reads, 4%) (Supplementary Figure S1C). Proteobacteria was the most abundant phylum (1,321,906 reads, 33% of total numbers of reads assigned to phyla), followed by Bacteriodiota (1,311,523 reads, 32%),

TABLE 3 PERMANOVA of the three gravel bars in low and high discharge.

Discharge	Df	SumsofSqs	MeanSqs	F Model	R2	Pr(>F)
Low	2	1.0656	0.53279	1.9491	0.15657	0.005
High	2	0.4433	0.72166	2.6171	0.2073	0.001

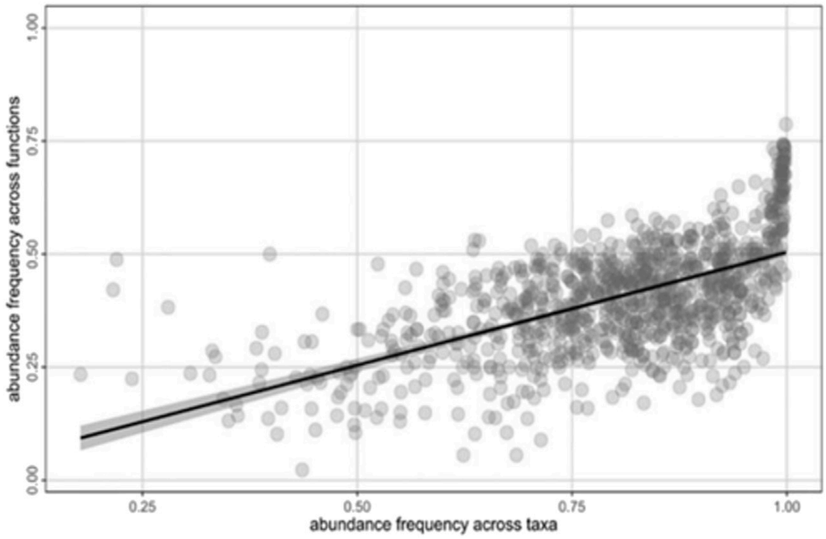

FIGURE 4
Mantel test analysis of abundance frequency based on taxa β-diversity versus abundance frequency based on putative metabolic functions using the Bray-Curtis index.

Verrucomicrobiota (269,793 reads, 7%), Acidobacteria (217,836 reads, 6%), and Actinobacteria (60,563 reads, 2%) (Supplementary Figure S1D).

In each gravel bar, the NMDS ordination (Figure 2A) showed clustering of the three hyporheic areas within the gravel bars at low discharge while such clustering could not be observed at high discharge using ASV-level (Figure 2C). PERMANOVA (Table 1) showed significant dissimilarity in the community structure among the three areas at low discharge (p = 0.004) but no significant difference at high discharge (p = 0.326). The NMDS results (Figures 2B, D) of the three gravel bars showed clustered patterns under both high and low discharge conditions. PERMANOVA revealed significant community divergence among the three gravel bars at low (p = 0.005) and high (p = 0.001) discharge (Table 2).

The alpha diversity chao1 richness, Shannon, and Simpson indices ranged between 35 and 4023, 3.18–7.33, and 0.002–0.471, respectively, among the 16 areas based on the ASV-level (Supplementary Table S2). We observed no significant difference between the alpha metrics between the areas within gravel bars under both low and high discharge conditions (Figures 2E, F).

The dbRDA results (Figures 3A, B) showed that turbidity (p = 0.002), EC (p = 0.001), and Al (p = 0.019) significantly influenced the microbial community structure as environmental factors at low discharge, while pH (p = 0.033) and Ca (p = 0.011) were the environmental factors influencing microbial communities at high discharge (Table 3).

Putative metabolic function of the hyporheic microbial communities

A total of 2,962 ASVs (15.12%) out of 5,453 ASVs were assigned to at least one putative metabolic function. We identified 67 out of 92 putative metabolic functions in the FAPROTAX database. Chemoheterotrophy and aerobic chemoheterotrophy obtained annotated putative metabolic function throughout the 16 areas (Supplementary Figure S2). Methanotrophy and methylotrophy were described as dominant in the downwelling areas while methanogenesis was dominant in the upwelling areas both at low and high discharge. Aerobic ammonia oxidation was the most abundant putative metabolic function identified at the intermediate area. We also described a significant positive correlation between beta diversity based on community structure and putative metabolic function structure (Figure 4).

Discussion

This study aimed to contrast the microbial community structure and putative metabolic function among the hyporheic, i.e., downwelling, upwelling, and intermediate areas within and among gravel bars between two (i.e., low and high) discharge levels of a dam-regulated river.

Community divergence among the three sampling areas

Our results revealed significant microbial community divergence among the three areas within the gravel bars under low discharge conditions. This could be attributed to local adaptation reflecting environmental heterogeneity among hyporheic areas within the gravel bar at low discharge. Moreover, we observed significant community divergence between 2-km distance gravel bars that remained even under high discharge conditions. However, we could not observe any significant divergence within the gravel bar areas under high discharge condition. The observed differences between the gravel bars could be attributed to their bar geomorphology and sediment characteristics (Ock et al., 2015). Since microorganisms are adapted to the local environment of each gravel bar and the geographic distance between the bars was relevant, inter-bar migration that could homogenise the microbial community structure among the bars was not evident regardless of the discharge level.

Our results also suggest that the microorganisms cannot disperse as far as 2 km even under high discharge but can only move strongly within gravel bar. The contrasting results of community divergence observed between two spatial areas, i.e., within and between gravel bar areas, provided valuable insights into the role of environmental heterogeneity in microbial community structure in the hyporheic zone at different spatial areas. Our observation is in accordance with Yang et al. (2021) observation that microbial species could still be detected within a 1-km distance downstream of the sampling site.

This significant finding underlines the similarity of microbial community structure among the three hyporheic areas observed under high discharge conditions. These results support our hypothesis that an increased river surface water discharge would also represent mean hydrologic changes in hyporheic zones. The disturbance among the hyporheic zone microbial communities might rise during the high discharge condition introducing homogenisation. This could be explained by the potential mechanism of mixing hyporheic water between the three areas. However, determining the driving process was not possible since the surface water was not examined. Understanding how communities respond to disturbances such as a flood is essential to identify biological and ecological processes that determine their assembly and predict future effects on diversity and function (Marmonier et al., 2012). To the best of our knowledge, this is the first study to investigate how increased river water discharge influences heterogeneous microbial communities among the hyporheic flow path in gravel bars.

Environmental factors shaped microbial community divergence

We demonstrated that turbidity, EC, Al, pH, and Ca were the environmental factors that significantly shaped microbial community divergence. Certain microbial community groups cannot withstand when metal concentrations increased in the environment. Moreover, metal concentrations play an essential role in influencing microbial communities (Zeglin, 2015). For example, Feris et al. (2003) described a significant relationship between streambed metal concentrations in hyporheic zone and microbial community structure in six different rivers. Turbidity is essential in water microbial communities as it influences the processes within the primary producers, such as phytoplankton and photosynthetic bacteria. These primary producers rely on light energy and oxygen production for growth and variable water chemical properties, that in turn, influence bacterial nutrient use in the river ecosystem (Wagner et al., 2015).

Our results showed that several water qualities, e.g., Turbidity, EC, pH, Al and Ca, were shown to be associated with microbial communities. The difference in water discharge is assumed to cause changes in environmental conditions in which water quality and microbial communities respond. However, the environmental variables associated with the microbial community may be temporal, and associated environmental variables maybe interchangeable depending on the flow magnitude and duration.

Putative functions involve in biogeochemical processes

Nitrification, denitrification and methanogensesis were involved in biogeochemical processes in the hyporheic zone. However, this study did not directly measure biogeochemical processes, so it should be noted that these identified functions were potential or putative ecological functions based on the 16S rRNA gene sequencing. We identified a dominant putative metabolic function at each hyporheic area (Supplementary Figure S2). Methanogenesis was abundant at the upwelling, while methanotrophy and methlylotrophy at the downwelling areas in both discharge levels. This study supported the with the findings of Jones et al. (2015) that methanogenesis accounted for all the respiration in anoxic sediments and 0.3%–0.6% of the total respiration. These findings implied that hyporheic zone is essential in the carbon cycle such as methylotrophy, methanotrophy and methanogenesis in gravel bars. Moreover, the hyporheic zone through methanogenesis appears to be an important pathway for organic cycling and is a potential source of labile organic carbon on the surface of stream water. Putative metabolic functions, chemoheterotrophy and aerobic chemoheterotrophy, were the most dominant throughout all the 16 areas, suggesting the importance of metabolically active microorganisms in hyporheic zone. Mainly the abundant bacteria (e.g., Proteobacteria, Acidobacteria, and Verrucomicrobiota) contributed to chemoheterotrophy and aerobic chemoheterotrophy as putative metabolic functions. Our study provided profiles of ecological functions across the different areas of gravel bars. Overall, our study also implies that hyporheic zone is suitable for thriving heterotrophic microorganisms.

Furthermore, we identified a positive correlation between differences in taxonomic composition and differences in potential metabolic functions (Figure 4). This finding implies that the taxonomic structure divergence observed between areas or gravel bars reflects different putative metabolic functions that emerged among the heterogeneous environments. This result is in good agreement with previous studies on stream microbial communities (Galand et al., 2018; Fasching et al., 2020; Serrana et al., 2022). However, it should be also noted that the use of 16S rRNA gene sequences to predict metabolic function is constrained by the limited information content of the amplicon and limited databases. Hence, the putative metabolic function would require further validation using metagenomics and metatranscriptomics analyses that could provide comprehensive information on functional genes.

We observed no significant difference in alpha diversity among any of the three areas in the three gravel bars under either low or high discharge conditions. This result coincided with those of Nelson, et al. (2019) and Sackett, et al. (2019), showing no significantly different variation level in microbial communities among the areas in the gravel bar. We consider that each area can harbor similar alpha diversity levels with species turnover among the areas. Potential mechanisms for the similar alpha diversity among the areas, such as the environmental capacity for the number of species that each area can hold or limit of the number of detectable species per area by metabarcoding, should be explored in future studies. Although the alpha diversity did not varied across gravel bars with low and high flow conditions, microbial community structure might have differences within gravel bar areas, given the environmental heterogeneity of hyporheic zones in the gravel bar.

Conclusion

In conclusion, spatial environmental heterogeneity among the hyporheic zone at low discharge resulted in microbial community structure divergence at three hyporheic (i.e., downwelling, upwelling, and intermediate) areas within the gravel bars. Our finding highlights how high discharge influences microbial community convergence, as explained by the homogenisation in hyporheic zones. Putative metabolic functions were identified in the three hyporheic areas, correlating with the taxonomic community structure, and were determined to understand the process of microbial ecology dynamics in hyporheic zones. Furthermore, we identified environmental factors such as turbidity, EC, and Al as drivers of divergence between hyporheic areas within gravel bars. To further understand the biological mechanisms of microbial communities in the hyporheic zone, we believe that future studies should focus on metagenomics and metatranscriptomics to understand better the functional genes and activity of microbial communities in the hyporheic zone in gravel bars. Moreover, further studies are recommended on a longer time scale to validate the influence of flow discharge on hyporheic microbial communities.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: https://www.ncbi.nlm.nih.gov/search/all/?term=PRJNA855985, PRJNA855985

Author contributions

AD-L: Conceptualisation, Methodology, Investigation, Data curation, Formal analysis, Visualisation, Writing–original draft. JS: Investigation, Formal analysis, Writing–review and editing. ST: Investigation, Data curation, Methodology, Writing–review and editing. YT: Investigation, Data curation, Writing–review and editing, Funding acquisition. KW: Conceptualisation, Writing–review and editing, Resources, Supervision, Project administration, Funding acquisition. 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/fenvs.2023.1205561/full#supplementary-material

SUPPLEMENTARY FIGURE S1
Microbial taxonomy and diversity for each hyporheic area **(A)** Top 10 most abundant genera. **(B)** Top 10 most abundant phyla. **(C)** Top five most abundant genera **(D)** Top 5 most abundant phyla.

SUPPLEMENTARY FIGURE S2
Heatmap showing the abundant putative metabolic function for each hyporheic area i.e., downwelling, upwelling and intermediate.

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Aquatic protected area system in the Qinghai–Tibet Plateau: establishment, challenges and prospects

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Conservation of wetlands on the Qinghai–Tibet Plateau is vital to the ecological security of China and even all of Asia. In this study, we investigated the aquatic protected area system established by the Chinese government in the Qinghai–Tibet Plateau. In general, 9 categories of aquatic protected areas have been established in this area, linked to the International Union for Conservation of Nature classification system of protected areas. The diverse main protection objectives of different protected areas have played a key role in wetland conservation. However, the protection of wetland environments and aquatic organisms has been insufficient in some atypical protected areas and local protected areas. We further constructed a list of important aquatic organisms in the Qinghai–Tibet Plateau and analyzed the protected status of those important species through gap analysis. A total of 156 important aquatic species were identified, with 8 gap species and 18 inadequately protected species. It is encouraging that none of the national key protected species are gap species, but there are 4 gap species that are threatened species on "China's red list". In addition, we found that 17 important species are designated as Data Deficient or Not Evaluated on "China's red list", including 8 national key protected species. Finally, we propose the prospects for solving the existing problems of aquatic protected area systems: integrating aquatic protected areas, enhancing the status of community-based conservation, and increasing investment in important aquatic organism research.

KEYWORDS

Qinghai–Tibet Plateau, aquatic protected area, aquatic organism, conservation gap, prospect

1 Introduction

In the global context, inland wetlands face threats of water quality deterioration (Rodell et al., 2018), habitat fragmentation (Harlan et al., 2021), loss of biodiversity (Dudgeon, 2019), etc. due to anthropogenic activities. Therefore, efficient wetland protection is essential to counter the increasingly severe crisis. Among protection methods, establishing protected areas is widely used and yields substantial results worldwide (Maxwell et al., 2020). Previous studies have confirmed that expansion of protected areas is significantly associated with increased biodiversity (Venter et al., 2014; Di Minin and Toivonen, 2015).

Protected areas are the specific geographic spaces established to achieve long-term conservation of nature, associated ecosystem services and cultural values, and are managed through legal or other effective means (Dudley, 2008). According to the classification system of the International Union for Conservation of Nature (IUCN), protected areas have 6 categories: strictly protected area (I), national park (II), natural monument or feature (III), habitat/species management area (IV), protected landscape/seascape (V) and protected areas with sustainable use of natural resources (VI) (Dudley, 2008).

The Qinghai–Tibet Plateau (QTP), known as the "Third Pole" and "Roof of the World", is a vital ecological buffer for China and even all of Asia. Many important rivers originate from here, which are home to a variety of unique aquatic organisms (Figure 1). However, high, cold environments make these ecosystems extremely fragile and lacking in self-regulation and repair abilities (Liu et al., 2021). In recent years, wetlands in the QTP have been severely damaged due to the intensification of anthropogenic impacts brought by economic activities (Xu et al., 2019a). Additionally, global climate change has intensified the warming and humidification of the QTP, which poses a potential environmental crisis (Kuang and Jiao, 2016; Chen et al., 2023).

In past decades, numerous protected areas have been established on the QTP, effectively protected the ecosystems in this region (Li et al., 2020; Zeng et al., 2020). Among the different types of protected areas, those established on waters were usually divided into two categories: marine and freshwater (Suski and Cooke, 2007). However, this classification excludes the inland saltwater, which leads to the omission of research and management data (Wanghe et al., 2024). In fact, there has been an increasing amount of literature on the wetland status and protection of the QTP (Zhao et al., 2015; Wang et al., 2020), but there is no discussion of the protected area system established on inland waters in this area. Moreover, a comprehensive and unified list of important aquatic organisms of the QTP is still lacking. The absence of such a list has resulted in limitations in previous studies at the data level (Wanghe et al., 2024).

To address the above concerns, we will (1) construct an accurate system of protected areas established on inland waters; (2) formulating the list of important aquatic organisms on the QTP; (3) analyze the progress and drawbacks of protecting aquatic organism on the QTP; (4) outline possible prospects for future research directions. Results of this study are expected to provide strong support for future researches and protection efforts on the QTP, which can also guide the establishment of similar systems in other regions over the world.

2 Materials and methods

2.1 Building of the aquatic protected area system

Based on our analysis, "aquatic protected area (APA)" is the most appropriate term for protected areas on inland waters. Data on APAs on the QTP from 1956 to 2018 were collected to build this system. China's protected areas are established by different government departments, most of which can be divided into national and local (provincial, municipal, county) levels (Xu et al., 2017). There are some APAs in which the main

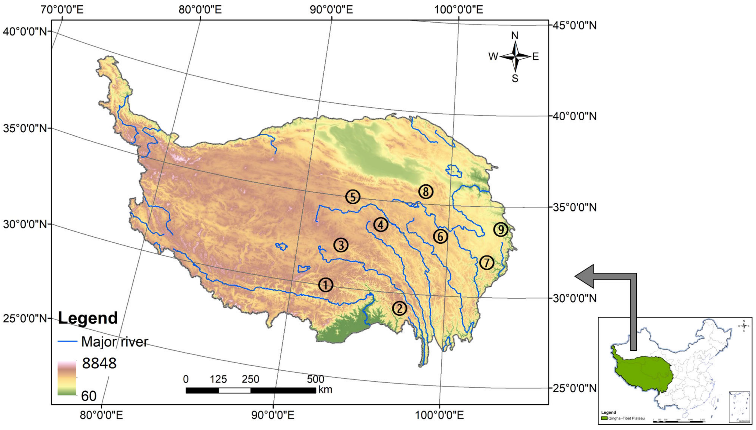

FIGURE 1
The elevation and core rivers (①: Brahmaputra River, ②: Irrawaddy River, ③: Nujiang River, ④: Lantsang, ⑤: Yangtze River, ⑥: Ya-lung River, ⑦: Dadu River, ⑧: Yellow River, ⑨: Minjiang River) of the Qinghai–Tibet Plateau. The data of the digital elevation model have systematic errors, because the highest value was higher than Mount Everest; however, this had no influence on this study.

protection target is not aquatic organism or wetland ecosystem, but the range covers important wetlands. We believe that these protected areas are just as important as the typical APAs, so we call them "atypical aquatic protected area (AAPA)". These consist of three categories: national park, nature reserve and world natural heritage.

In China, national parks, nature reserves and nature parks are the core elements in the future national protected area system (General Office of the CPC Central Committee, and General Office of the State Council of the People's Republic of China, 2019). In addition, there are nine other categories of APAs in China (Table S1). Due to data limits, this paper cannot provide comprehensive statistics for all kinds of APAs. Therefore, we analyzed the number and distribution of national parks, nature reserves and wetland parks (a kind of nature park) on the QTP. All protected areas data were acquired from the China's National Forestry and Grassland Administration database.

2.2 Formulating the list of important aquatic organisms

We selected fish, mammals, invertebrates and macrophytes as the target aquatic taxa. Species inclusion criteria for the list were put forward through expert consultation. The specific criteria were as follows:

(1) Fish, mammals and macrophytes were endangered from vulnerable (VU) to extinct in the wild (EW) on "China's red list of biodiversity" (Ministry of Ecology and Environment, PRC., and Chinese Academy of Sciences, 2013, 2015; Zhang and Cao, 2021), and invertebrates were endangered from VU to EW on "China species red list, Vol. III, Invertebrates" (Wang and Xie, 2005). Hereafter, these two lists are collectively known as "China's red list".

(2) Species were included in the "national key protected wild animal list" (National Forestry and Grassland Administration, and Ministry of Agriculture and Rural Affairs, PRC, 2021a) and the "national key protected wild plant list" (National Forestry and Grassland Administration, and Ministry of Agriculture and Rural Affairs, PRC, 2021b).

(3) Other species were included if they had important ecological, scientific, or social value.

2.3 Protected status analysis of important species

First, we counted the distribution of each species with counties as the basic distribution unit, and species with a distribution range of no more than five counties are defined as "narrowly distributed species"; then, we mapped the distribution of important aquatic species.

Gap analysis is an efficient tool to indicate the protected status of species (Scott et al., 1993; Li and Pimm, 2020). To achieve this goal, we overlaid the distribution maps of each species with the distribution maps of the wading reserves. Species that are not covered by aquatic protected areas are defined as "gap species". Local protected areas in China may encounter problems in management and resource allocation (Ma et al., 2019). Moreover, protected areas with sustainable use of natural resources, such as wetland parks, provide lower protection intensity than national parks and nature reserves. For the above reasons, the protection of important species should follow the principle of prioritizing national parks or national nature reserves. Species that are covered by other aquatic protected areas are defined as "inadequately protected species".

Species distribution data were acquired from the "China's red list", the IUCN database (https://www.iucnredlist.org/), the "National Specimen Information Infrastructure of China" (http://nsii.org.cn/2017/home.php), the "National Tibetan Plateau Data Center" (https://data.tpdc.ac.cn/home), and the "Report on advances in Tibetan plateau research (2009–2010, 2012–2013)" (China Association for Science and Technology, 2010, 2014). During the data collection process, we found that some data were outdated, and the survival status of some species still unclear. This limitation undoubtedly affects the scope of this study.

It must be emphasized that all the data used in this study are publicly available data.

3 Results

3.1 Composition of the aquatic protected area system

The APA system contains seven categories of nationally constructed protected areas, as well as internationally important wetlands designated by the Ramsar Convention and world natural heritage designated by the World Heritage Convention (Table 1). Remarkably, these APAs contain all six categories of protected areas of the IUCN classification system.

Among the 10 pilot national parks in China, Three-River-Source National Park, Qilian Mountain National Park, Giant Panda National Park and Patatson National Park are completely or partially located on the QTP. According to incomplete statistics, there are 60 aquatic nature reserves and 19 wetland parks in this area, which contains 21 national nature reserves and 11 national wetland parks (Table 2). Except for the Three-River-Source National Park, the remaining three national parks are AAPAs, and there are 25 atypical aquatic nature reserves in this area (Figure 2B, Table S2). The primary protection targets of these nature reserves consist of forest ecosystems, geological heritage and terrestrial wildlife.

Figure 2A shows that eastern and central regions are the main distribution areas of APAs. On the watershed side, APAs have a high cover degree on the Irrawaddy River, Lantsang, Yangtze River, Ya-lung River, Dadu River, Yellow River and Minjiang River,

TABLE 1 Types of aquatic protected areas in the Qinghai–Tibet Plateau.

Protected areas in the Qinghai–Tibet Plateau	Management agency/implemented convention	IUCN categories
National park	NFGA	II
Nature reserve	NFGA	I
Wetland park	NFGA	V
National importance wetland	NFGA	VI
Water conservancy scenic spot	MWR	V
Drinking water source protection area	MWR	VI
Aquatic germplasm resources protection zone	MARA	IV
International importance wetland	RC	VI
World natural heritage	WHC	III

NFGA, National Forestry and Grassland Administration; MARA, the Ministry of Agriculture and Rural Affairs; MWR, the Ministry of Water Resources; RC, Ramsar Convention; WHC, World Heritage Convention.
The internationally important wetland and world natural heritage were managed by the NFGA in China.

whereas the Brahmaputra River and Nujiang River are covered by few APAs.

3.2 Composition of important aquatic organisms

The list of important aquatic organisms in the QTP included 111 species of fishes, 4 species of mammals, 20 species of invertebrates and 21 species of macrophytes (Table 3). Table S3 shows that there are 120 endemic species in China, including 28 endemic species on the QTP (23 species of fishes, 4 species of invertebrates and one macrophyte).

From the statistical results, a total of 134 (85.9%) important species were classified as critically endangered (CR), endangered (EN) or VU in China's red list, containing 103 species of fishes, 3 species of mammals, 9 species of invertebrates and 19 species of macrophytes (Table 3). Moreover, there were 57 national key protected species on our list, including 39 species of fishes, 4 species of mammals, 2 species of invertebrates and 12 species of macrophytes (Table 3).

TABLE 2 Composition of aquatic nature reserves and wetland parks in the Qinghai–Tibet Plateau.

Protected area level	Nature Reserve	Wetland Park
National	21	11
Provincial	24	8
Municipal	5	–
County	10	–
Total	60	19

It is apparent from Figure 3 that only 44 (32.8%) threatened species (threat level from VU to CR) in our study are national key protected species, and 8 national key protected species in our study are still Data Deficient or Not Evaluated by China's Red List.

3.3 Distribution of important aquatic species

Spatial distribution data reported that there are 33 narrowly distributed species (Table S3). The important species mainly live in the eastern region, where the density is significantly higher than in the western and northern regions (Figure 4A). Specifically, important fishes mainly live in the eastern and northern regions (Figure 4B). The distribution of mammals and macrophytes both showed a clear spatial pattern of decreasing from south to north; therefore, macrophytes are mainly distributed in areas other than the Tibet Autonomous Region (Figure 4C, E). In addition, invertebrates are only distributed in parts of the eastern and southern regions (Figure 4D). We found that only a minority of important species live in the Brahmaputra River but this includes many national key protected species, which is a remarkable result.

3.4 Protection status of important aquatic organisms

Our study showed that APAs protect taxa to different extents. There are 8 gap species and 18 inadequately protected species on the QTP through the GAP analysis (Figure 5). For important fishes, there is one gap species and 13 inadequately protected species (Figure 5). For important invertebrates, there were 7 gap species and 2 inadequately protected species; in addition, there were 3 inadequately protected macrophyte species (Figure 5).

Encouragingly, none of the national key protected species are gap species, but 4 of the gap species are threatened species on the "China Red List", in which *Polycelis lhunzhubica* and *P. sinensis* are endemic species of the QTP (Table 4, Table S3). Of all the inadequately protected species, there are 5 national key protected species and 15 threatened species on the "China Red List" (Table 4). Among them, *Isoetes hypsophila* is not only a first-class protected species in China and a threatened species, but also an endemic species of the QTP (Table S3). *Percocypris retrodorsalis* and *Ottelia acuminata* var. *acuminata* are second-class protected species in China. Moreover, there are 6 endemic species of the QTP, excluding *I. hypsophila* (Table S3).

4 Discussion

4.1 Achievements of the protection service

The number of protected areas in China growing fast. By 2018, China had established more than 12 000 protected areas

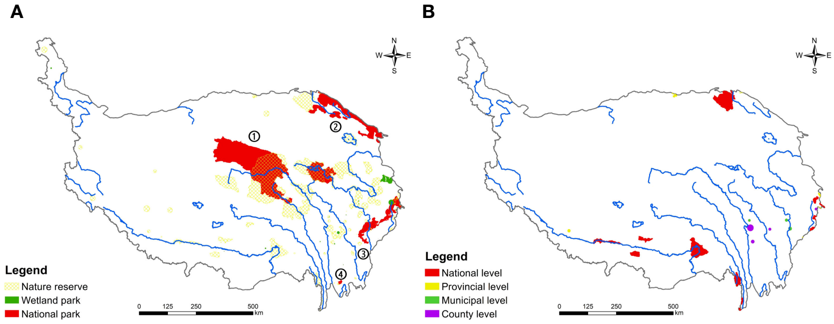

FIGURE 2
Distribution of aquatic protected areas in the Qinghai–Tibet Plateau. **(A)** Main types of aquatic protected areas (①: Three-River-Source National Park, ②: Qilian Mountain National Park, ③: Giant Panda National Park, ④: Patatson National Park), **(B)** Atypical aquatic nature reserves.

TABLE 3 Endangered level in China's red list and national protection level of important aquatic organisms in the Qinghai–Tibet Plateau.

	Threaten/ Protected Level	Fish	Mammal	Invertebrate	Macrophyte	Total
Endangered level in the China's Red List	CR	11	–	–	1	12
	EN	43	3	3	7	56
	VU	49	–	6	11	66
	NT	3	–	–	1	4
	LC	1	–	–	–	1
	DD	2	–	–	–	2
	NE	2	1	11	1	15
	Total	111	4	20	21	156
National protection level	Level I	5	1	–	2	8
	Level II	34	3	2	10	49
	Total	39	4	2	12	57

(Ouyang et al., 2018), covering more than 50.3% of the natural wetlands (National Forestry and Grassland Administration, 2020). To protect this critical area, an effective protected area system was established on the QTP (Table 1). Existing system fulfilled different protection objectives and effectively protected most of the wetlands (Figure 2). Against a backdrop of national park system construction in China, the central government has integrated the top-level design and management departments for the whole protected area system (Xu et al., 2019b). This measure obviously reduces the negative impact of multi-management in the construction and management. Another remarkable achievement was that aquatic organisms in the QTP have been well protected by APAs according to our analysis (Table 4, Figure 5).

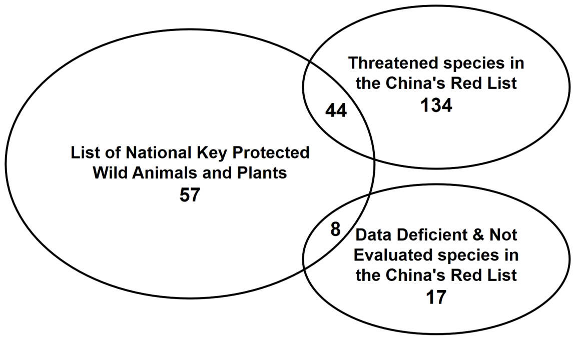

FIGURE 3
Coupling of China's red list with the national key protected wildlife list.

4.2 Challenges in current protection efforts

4.2.1 Protection efforts are uneven across protected areas

Based on the "Regulations of the People's Republic of China on nature reserves", nature reserves were divided into core zones, buffer zones and experimental zones (China's State Council, 1994). Due to the differences of main protection objectives, wetlands within the

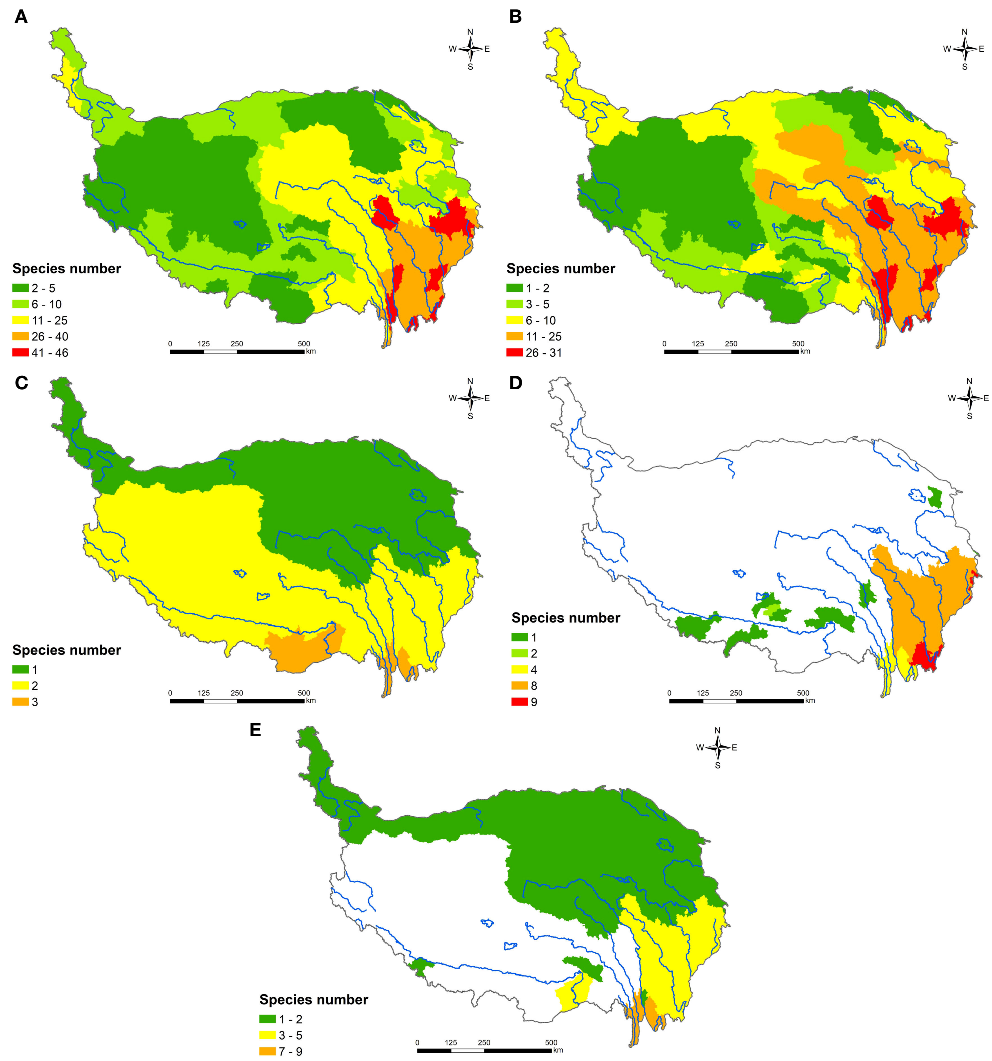

FIGURE 4
Distribution of important aquatic organisms in the Qinghai–Tibet Plateau (**A**: Total species, **B**: Fish, **C**: Mammal, **D**: Invertebrate, **E**: Macrophyte).

nature reserve may not be covered by the core zone when planning the atypical aquatic nature reserves. As a result, the protection of wetland ecosystems and aquatic organisms in protected areas is insufficient.

Both typical and atypical APAs occur at the national and local levels in China (Xu et al., 2017). Compared with national protected areas, local protected areas have been more prone to problems such as lack of funds, mismanagement, and illegal development for economic development (Ma et al., 2019). As an economically underdeveloped area in China, these problems may be even more serious on the QTP.

4.2.2 Gaps in the protection service

Although the APA system on the QTP is constantly improving as the coverage rate increases, there are still some conservation gaps. For example, the Brahmaputra River is crucial to the lives of people within its watershed. Therefore, it is essential to protect this watershed (Huang et al., 2009). However, the size and number of protected areas in the watershed do not match the protection needs (Figure 2). In addition, plateau lakes such as Namco Lake and Mapam Yamco Lake and Yamzho Yumco Lake are considered "holy lakes" in the beliefs of local residents (Li et al., 2014). However, the reality is that the coverage rate of APAs in these lakes still low (Figure 2).

As the highest and largest lake group in the world and the source of many important rivers, the lakes and rivers on the QTP are of great ecological value (Liu et al., 2021). Various rare and endemic organisms live in them. There are, however, some threatened species, and key protected species are gap species or inadequately protected species (Table S3, Figure 5). This situation provides a warning that existing APAs do not provide adequate protection for important aquatic species in the area.

Surprisingly, there are 17 important species are data deficient or not evaluated on "China's red list", including 8 national key protected species (Table 3, Figure 3). The status of these species still unknown. In fact, they may already be under serious existential threat. Furthermore, some data has not been updated for a long time (Zhang and Cao, 2021).

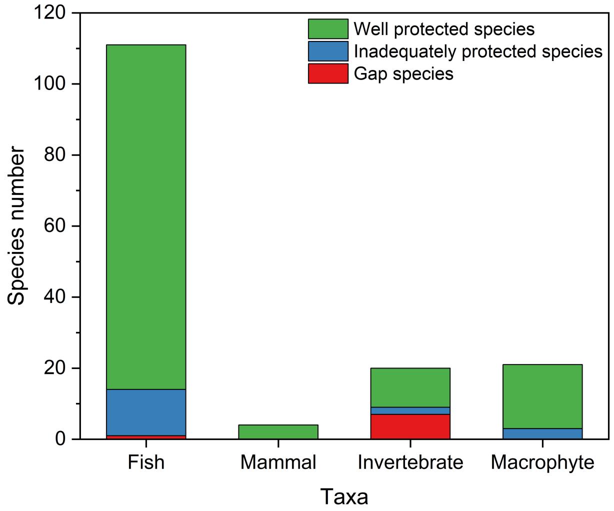

FIGURE 5
Protected status of important aquatic organisms in the Qinghai–Tibet Plateau.

4.3 Prospects

4.3.1 Integration of aquatic protected areas

The QTP is one of the regions with the richest biodiversity in China, and the southeastern region in this area has the highest species richness (Fu et al., 2021). We found that most of the APAs in the southeastern region are small and distributed in a spotty pattern, providing low protection efficiency for wetland ecosystems (Figure 2). It is efficient and feasible to consolidate the ecological barrier function of the QTP by establishing national park groups (Fu et al., 2021). As mentioned in Fu et al. (2021), the "national park group on the southern flank of the Eastern Himalayan Mountain plate" will be one of the major groups on the QTP.

It is well known that the QTP borders several countries, causing a large amount of wildlife to be transregionally distributed. Conservation cooperation between countries is particularly important to protect transboundary landscapes and mitigate biodiversity loss (Bawa et al., 2010). China has established at least 17 cross-border protected areas to date, which have achieved preliminary success (Tang et al., 2016). To develop the protection effect of the APA system, additional work will be needed to establish more cross-border protected areas in this region (Bawa et al., 2010; Fu et al., 2021).

TABLE 4 Protected status and threatened status for gap species and inadequately protected species in the Qinghai–Tibet Plateau.

	Taxa	National protected species	Threatened species
Gap species	Fish	–	1
	Invertebrate	–	3
Inadequately protected species	Fish	3	11
	Invertebrate	–	1
	Macrophyte	2	3

4.3.2 Enhance the status of community-based conservation

Recent study shows that the growth of the human footprint may compromising the benefits of protected areas on the QTP (Hua et al., 2022). Therefore, balancing protected areas with human activities is the main option for protection work (Gibson and Marks, 2000; Balint, 2006). Herdsmen on the QTP have a high enthusiasm for participating in protection work. This enthusiasm derives from their belief and custom of respecting nature, which has been formed thousands of years. In the practice of the Three-River-Source National Park, the participation of the herdsmen community achieved good results (Zhao et al., 2018; Guo et al., 2023). Based on this, more community protected areas, such as "feng-shui forests", should be established. This policy may provides a satisfactory solution to the conflict between conservation and development (Shen et al., 2012; Huang et al., 2021). Besides, residents' beliefs, customs, and values should be fully respected during the conservation (Measham and Lumbasi, 2013).

High levels of water use for agriculture and livestock may pose a potential risk to the APAs and aquatic organisms. To tackle this problem, it is essential to evaluate the ecological and agricultural value of the water resources (Hatamkhani et al., 2022). After that, a balance must be found between water conservation and economic benefits. Water management programs are developed based on equilibrium flows. Due to the complex composition of water resources in this area, big data and model simulations can provide more accurate results (KhazaiPoul et al., 2019; Hatamkhani and Moridi, 2023).

Finally, compensation should be provided to farmers and herders whose economic interests have been jeopardized due to conservation efforts. This policy ensures that the benefits of these efforts are shared equitably (Measham and Lumbasi, 2013).

4.3.3 Increasing the research investment in aquatic organisms

The results of our study must be interpreted with caution because some numbers and distribution data of species were outdated, and the status of some species remains unclear. This statement suggests that there are deficiencies in the research on aquatic organisms for QTP. Previous studies have indicated that effective biodiversity protection and establish effective protected areas rely on various regional research (Batisse, 1997; Hu et al., 2019). To fill the research gap, further research should be undertaken to investigate the populations and habitats of important species. Importantly, the research must be continuous, especially for flagship species, umbrella species, key species, and narrowly distributed species. Meanwhile, a system capable of managing big data, updating and sharing detailed information in real-time is necessary (Li and Pimm, 2020; Bravo et al., 2021).

5 Conclusions

In this study, we reported on the status of the APA system on the QTP and provided information on prospects for future development. First, China has established an effective APA system in this area. However, conservation gaps persist. Specifically, the protection of AAPAs and local protected areas remain insufficient and likely to result in management problems. Further investigation showed that some threatened species are gap species, and some national key protected species and threatened species are inadequately protected species. It should be noted that our study was limited by the lack of specific and current data on some important species. To solve those problems and improve protection efficiency, what is now needed are: (1) integration of protected areas through the establishment of national parks and transnational protected areas; (2) enhancement of the strength of community-based conservation; and (3) increasing investment in the research on important species and the establishment of data management system. The findings in this study provided some new insights for the future wetland protection efforts on the QTP, and can guide the establishment and management of protected areas in other similar regions worldwide.

Data availability statement

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

Author contributions

HL was responsible for the analyses and interpretation of the data and wrote the original draft. LT was responsible for the field investigation, data collection and collation. XL conducted the field investigation. QC was responsible for administration and supervision of the project, writing-review and editing, and contributed to the conception of the research. 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.2024.1204494/full#supplementary-material

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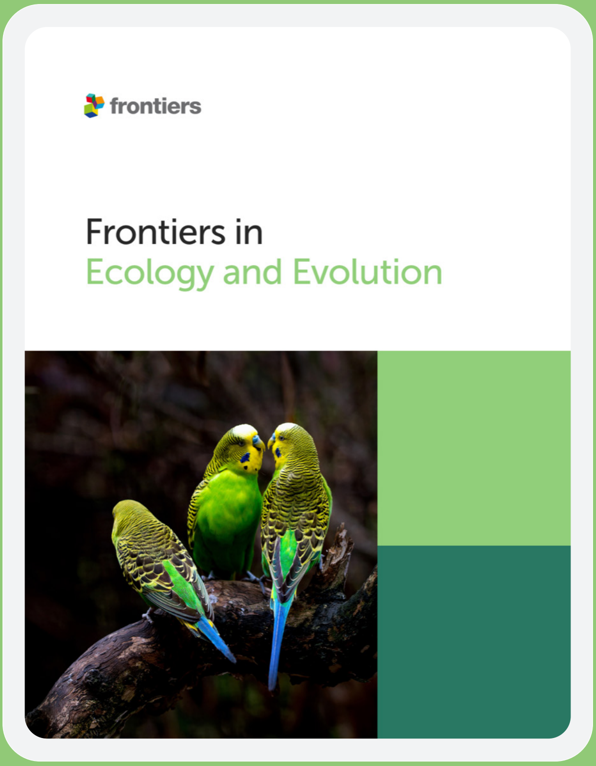

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