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New shortcut for conservation: The combination management strategy of "keystone species" plus "umbrella species" based on food web structure

Qiang Wang [a], Xingchun Li [b], Xuehong Zhou [b,*]

[a] Key Laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, Jilin Province 130102, China

[b] College of Wildlife and Protected Area, Northeast Forestry University, Harbin, Heilongjiang Province 150040, China

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ABSTRACT

In our protection efforts, it is urgently needed to adopt precise and efficient management measures to address the challenges brought by biodiversity loss. Keystone and umbrella species are one of the most widely used surrogate species concepts. Keystone species often determine the stability of food web. Umbrella species, often the top predators and further influencing the integrity of the food web. Conservation efforts relying on a single surrogate species often face limitations. In order to seek complementary and optimized management strategies, we innovatively combining the concepts of two surrogate species, propose the hypothesis that "keystone species plus umbrella species reflect the stability and integrity of the food web respectively, so the combination of them is the most suitable combination for the overall protection of the food web", and conducted validation research in a typical herbaceous marsh ecosystem. We constructed a typical food web model by using stable isotope, centrality indices and umbrella species strength index were used to quantitatively determine the keystone and umbrella species. Finally, we randomly paired nodes within the food web and remove different node pairs to investigate the impact of removal on the robustness of the food web, further validate the hypothesis. Our results indicated that when the node pair of "aquatic insects (keystone species) and top predatory catfish (*Silurus asotus*) (umbrella species)" was removed, the network efficiency reached its lowest point. This result confirmed our hypothesis, proposed a novel combination management strategy, which contribute to the development of more efficient and comprehensive biodiversity conservation decisions.

1. Introduction

Global biodiversity is being lost at an unprecedented rate, while the pressures causing this decline continue to intensify. The resulting impacts are significant, leading to the severe degradation of the quality and functionality of ecosystems that play a crucial role in environmental functionality and human health (Shin et al., 2022). While efforts are being made to mitigate the negative consequences of biodiversity loss, ensuring the integrity of ecosystems is of utmost importance, aligning with the emphasis placed in The UNFCCC Paris Agreement, under Decision 1/CP.21 (Shin et al., 2022). Throughout the course of balancing this relationship, scholars have increasingly recognized that the food web offers a natural framework for comprehending the intricate interactions among species and harmonizing the interplay between biodiversity and the quality and functionality of ecosystems (Thompson et al., 2012). It not only offers diverse perspectives for ecosystem research based on different themes (Gini et al., 2022), but also has been widely recognized for its potential in guiding ecosystem management and species conservation (Tylianakis et al., 2010; Dobson et al., 2009). The food web, composed of interconnected trophic levels, resembles a towering building that requires a sturdy foundation and a complete roof to stand as a resilient structure. In other words, a stable and intact food web is crucial for maintaining high-quality ecosystems.

Scholars have made various beneficial attempts in conservation efforts centered around the food web. To optimize the availability of limited management resources, conservation biologists have proposed the strategies of management based on surrogate species approaches, including flagship, keystone, indicator, focal, and umbrella species, in order to find conservation shortcuts (Favreau et al., 2006). Surrogate species can be used to represent the needs of a broader range of species when the goal is to provide appropriate protection for the entire suite of species within a region (Wiens et al., 2008), thus necessitating their

* Corresponding author at: College of Wildlife and Protected Area, Northeast Forestry University, 26 Hexing Road, Xiangfang District, Harbin, Heilongjiang, China.
E-mail address: xuehong_zhou2012@nefu.edu.cn (X. Zhou).

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identification and utilization in the conservation biologist's toolbox (Valls et al., 2015). However, as research on surrogate species, including their conceptualization, selection methods, and effectiveness assessment, continues to advance, some issues have begun to arise with attempts based solely on individual surrogate species, given that each surrogate species carries different conservation implications and priorities (Meurant et al., 2018; Roberge and Angelstam, 2004).

Taking the three most prominent categories of surrogate species as examples, umbrella species have been recognized as an effective approach for managing communities by focusing on the needs of a wide range of species. The concept of umbrella species emphasizes providing a "protective umbrella" for other co-occurring species (Haemig, 2001), top vertebrate predators are often umbrella species due to their wide home ranges (Natsukawa and Sergio, 2022; Ripple et al., 2014; Li et al., 2023). One consequence of this tendency is that conservation management based on umbrella species places greater emphasis on top-down protection of ecosystems, often lacking consideration for stability, and there has been ongoing controversy regarding the determination and effectiveness assessment of umbrella species (Maslo et al., 2016). The concept of keystone species can address this limitation. Keystone species, relative to their abundance, who have disproportionately large impacts on the structure and functioning of ecosystems (Paine, 1969). The loss or extinction of keystone species can lead to significant changes in biodiversity and food web stability compared to other species (Libralato et al., 2006; Lindenmayer and Westgate, 2020). Keystone properties can be quantified using removal experiments based on food webs. In contrast to the concepts of umbrella species and keystone species, the selection of flagship species is not solely based on ecological importance but often influenced by social and cultural factors (Thornton et al., 2016; Kalinkat et al., 2017; Lindenmayer and Westgate, 2020). As one of the essential tools in conservation marketing, flagship species can attract public interest in conservation issues, and enhance the ability to secure funding and public support (Caro, 2010; Clucas et al., 2008). Attributes such as charisma and aesthetic features are commonly associated with flagship species (Lundberg and Arponen, 2022), but this approach often faces criticism due to skewed priorities (Veríssimo et al., 2014).

In summary, the numerous attempts to assess the performance of surrogate species have revealed some limitations. One of these is that focusing on a single surrogate species often fails to protect all co-occurring species due to different priorities (Roberge and Angelstam, 2004). As mentioned by Meurant et al. (2018) in their research, multiple surrogate species are better than any single surrogate species. In this context, starting from the perspective of food web integrity and stability, we aim to find a management approach that can maximize conservation benefits by selecting the fewest possible combinations of species for conservation actions. After considering several concepts of surrogate species, we preliminarily believe that the combination of keystone species and umbrella species can best reflects the integrity and stability of the food web. On the one hand, this combination effectively indicates food web stability through the keystone species as a cornerstone. On the other hand, the top predator, as a suitable umbrella species, tends to be the best representation of food chain length. It not only reflects the vertical structure of the food web (Schoener, 1989), but is also associated with other species within the food web, further influencing the functional integrity of the food web (Duffy et al., 2005). Therefore, combining the concepts of this combination and the idea of improving conservation efficiency, we innovatively propose the hypothesis that "keystone species plus umbrella species is the most suitable combination to reflect the stability and integrity of the food web" and we have conducted validation research in a typical herbaceous marsh ecosystem in northeastern China.

The research was primarily conducted in the following three aspects. Firstly, based on carbon and nitrogen stable isotopes, we constructed a food web model for the typical herbaceous marsh ecosystem in the Honghe region. Secondly, we weighted the links within the food web using species feeding rates and determined the keystone species within the food web based on degree centrality, betweenness centrality, and closeness centrality. The effectiveness of the centrality indices was further validated through sequential removal experiments. The umbrella species in the food web were determined using a recently developed index umbrella species strength that integrates degree, strength, and trophic level (Li et al., 2023). Based on this, we obtained a more accurate ranking for species prioritization in management. Lastly, based on the important hypothesis proposed in this study, we randomly paired species within the food web and conducted node pair removal experiments on 55 species combinations to explore the effects of different combinations removal on the robustness of the food web, further validating the hypothesis. The results of this study not only have the potential to optimize current conservation management strategies and facilitate efficient biodiversity conservation efforts but also provide new insights for maintaining stable and intact food webs.

2. Methods

2.1. Study area

Honghe National Nature Reserve is located within the boundaries of Tongjiang City and Fuyuan City in the Sanjiang Plain. It was included in the "List of Wetlands of International Importance" as early as 2002. As a microcosm of the original wetlands in the Sanjiang Plain, it preserves the largest area of marshland in China, making it one of the most diverse and well-preserved original wetlands in the country (Wang et al., 2020). The wetland area in the reserve is 190.41km^2 (National Forestry and Grassland Administration, 2022), which can be classified into four types, herbaceous marsh wetland is one of the main types. Honghe Reserve is highly representative and typical within the Sanjiang Plain and even within the same bioclimatic zone globally. The reserve exhibits a rich biodiversity, encompassing nearly all species found in the Sanjiang Plain (Zhu and Zhang, 2021). It is also an important breeding ground for the oriental white stork (*Ciconia boyciana*). Therefore, considering the high representativeness and conservation significance of this ecosystem, this study selected to carry out a representative case study in Honghe National Nature Reserve.

2.2. Sample collection and processing

This study conducted sample collection in the typical herbaceous marsh ecosystem of Honghe National Nature Reserve during June to July of both 2019 and 2020 (Fig. S1). A total of 63 representative species samples in the water body were collected, including representative fish like yellow catfish (*Pelteobagrus fulvidraco*, YC), catfish (*Silurus asotus*, C), amur sleeper (*Perccottus glenii*, AS), crucian carp (*Carassius auratus*, CC), amur weatherfish (*Misgurnus mohoity*, AW), amur minnow (*Rhynchocypris lagowskii*, AM), aquatic insects (AI), mudsnail (*Cipangopaludina chinensis*, M), zooplankton (Z), particulate organic matter (POM), and aquatic plant (AP). The basic information of the collected samples is presented in Table S1. The representative fish samples in this study corresponded to the species in the study of Zhao (2005), indicating that the collected typical species samples could effectively represent the basic information of the typical herbaceous marsh ecosystem in Honghe National Nature Reserve. Samples were stored at low temperatures for further processing in the laboratory.

In the laboratory, species identification work was conducted first, followed by sample pretreatment. For fish samples, the dorsal muscle portion was taken. Aquatic insect samples also collect the muscle portion. For mudsnail samples, the gut contents were emptied, and the gastropod muscle was collected. Zooplankton samples were placed in a glass dish, impurities were picked out, the gut contents were emptied overnight in distilled water, and the resulting water sample was filtered using a microporous membrane (45 μm). POM samples were filtered onto pre-combusted (450 °C for 4 h) glass fiber filters (Whatman GF/C) using a vacuum pump after filtering the water sample. Aquatic plant samples were rinsed with distilled water to remove decomposed leaves. Then, all pretreated samples were placed in a drying oven at 60 °C for 12–24 h until a constant weight was reached. They were ground into fine powder with a mortar and pestle, passed through a 100–mesh sieve, and stored in a drying oven in centrifuge tubes for further analysis. The study was approved by the Ethics Committee of the first author's organization (2023616).

2.3. Stable isotope analysis

The stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ of each samples were analyzed by using an elemental analyzer (Flash 2000, Thermo Fisher Scientific, USA) and a stable isotope mass spectrometer (Thermo Scientific MAT 253, Finnigan, Germany) at the Public Technology Service Center of the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences.

$$\delta X(‰) = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 1000 \quad (1)$$

The stable isotope ratios were expressed in delta (δ) notation, X represents ^{13}C or ^{15}N, R represents the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

2.4. Data processing and analysis

2.4.1. Trophic level calculation

Trophic level (TL) reflects the nutritional relationships among species within a system and the relative position of organisms in the food web (Lindeman, 1991).

$$TL = \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})}{\Delta^{15}N} + \lambda \quad (2)$$

$\delta^{15}N_{consumer}$ represents the nitrogen stable isotope value of consumers, $\delta^{15}N_{baseline}$ represents the nitrogen stable isotope value of baseline species, which is usually a primary producer or primary consumer. Previous studies have shown that the $\delta^{15}N$ of benthic invertebrates is more stable and can more accurately reflect the stable isotope characteristics of the habitat compared with phytoplankton and zooplankton (Chen et al., 2016). Therefore, mudsnail, a species with stable feeding habits and perennial existence in the Honghe National Nature Reserve, was chosen as the baseline species with a trophic level value of 2 ($\lambda = 2$). $\Delta^{15}N$ represents the trophic enrichment factor and is typically assigned a value of 3.4 ‰ (Post, 2002).

2.4.2. Food web model construction

In this study, the MixSIAR in R 4.1.2 was utilized to quantitatively determine the contribution of food sources to the consumers using Bayesian mixing models (Stock and Semmens, 2013). For the consumer types in this study, trophic enrichment factors (TEF) were determined based on previous research, with $\Delta^{13}C$ and $\Delta^{15}N$ values set at 1.3 ± 0.3 ‰ and 3.3 ± 0.26 ‰ respectively (McCutchan Jr et al., 2003; Kundu et al., 2021). Additionally, the Markov chain Monte Carlo (MCMC) run length was set as “Very long” and the error structure was defined as “Residual Only”. Finally, Gelman and Geweke diagnostics were used to assess the convergence of the model results.

2.4.3. Quantitative determination of umbrella species

Referring to the method of quantitative determination of umbrella species in the study by Li et al. (2023), umbrella species were determined based on the food web, linking species with different spatial requirements through predation relationships. The umbrella species strength index, which integrates degree, strength, and trophic level, was used to quantify the determination of umbrella species.

$$\text{Umbrella species strength}(i) = k_i \times (s_i/k_i)^{\alpha} \times TL = k_i^{(1-\alpha)} \times s_i^{\alpha} \times TL \quad (3)$$

k_i represents the number of adjacent nodes to node i, S_i represents the sum of weights of edges connected to node i (%). α is a positive tuning parameter, referring to the studies by Opsahl et al. (2010), an empirical value of 0.5 is used for α. TL represents the trophic level of each species.

2.4.4. Quantitative determination of keystone species

In this study, we refer to the concept of shortest paths as summarized by Dijkstra (1959), where the feeding rates between species are considered as the link weights to calculate the shortest paths between nodes (Xing et al., 2021).

$$dw(i,j) = min(1/w_{ih} + \ldots\ldots + 1/w_{hi}) \quad (4)$$

$dw(i,j)$ represents the shortest distance from node i to node j, and w_{ih} denotes the weight passing through node i. The link weight is defined as the feeding rate between species in this study.

2.4.4.1. *Degree centrality.* Degree centrality is the most straightforward measure of centrality that characterizes the centrality of nodes in a network. In a directed network, degree centrality is the sum of the in-degree and out-degree of a node.

$$D_i = D_{in,i} + D_{out,i} \quad (5)$$

D_i represents the degree centrality of node i, $D_{in,i}$ represents the total number of links pointing to node i, and $D_{out,i}$ represents the total number of links originating from node i.

2.4.4.2. *Betweenness centrality.* Betweenness centrality is a measure used to quantitatively analyze the control ability of species over information exchange in a network (Freeman, 1977).

$$B_i = \sum_{v \neq i \neq j} \sigma_{vj}(i) \quad (6)$$

B_i represents the betweenness centrality of node i. σ_{vj} denotes all the shortest paths between v and j, while $\sigma_{vj}(i)$ represents the number of shortest paths between nodes v and j that pass through node i.

2.4.4.3. *Closeness centrality.* Closeness centrality is a measure used to indicate the extent to which a species has an advantage in transmitting information within a network (Okamoto et al., 2008).

$$C_i = \sum\nolimits_{i \neq j}^{n} d_{ij} \quad (7)$$

C_i represents the closeness centrality of node i, and d_{ij} is the shortest path length between i and j.

2.4.5. Sequential removal approach

2.4.5.1. *Topological approach.* In order to more accurately identify the effectiveness of the three centrality indices (degree centrality, betweenness centrality, and closeness centrality) in determining keystone species, and to find the most accurate method for determining keystone species, we employed the widely accepted topological removal approach for sequential removal (Sun et al., 2020; Melián and Bascompte, 2010). Based on the calculation results of the above three centrality indices, the species in the food web were sorted. Four scenarios were used to determine the priority of removal: (1) removing nodes in descending order of degree centrality, (2) removing nodes in descending order of betweenness centrality, (3) removing nodes in descending order of closeness centrality, and (4) random removal of nodes. The robustness of the network was observed during the iterative process of node removal. Each sequence removal was repeated until no secondary extinctions occurred, and then the next round of sequence removal was initiated. When a species loses all its resources, it is considered as a secondary extinction. Primary producers, assumed to be aquatic plant in this study, do not undergo secondary extinctions (Dunne and Williams, 2009; Dunne et al., 2002).

2.4.5.2. Network robustness measures. In this study, the relative size of maximum connected subgraph in the network was used to measure the changes in network robustness during the sequence removal process. It is often used to indicate the extent of damage to the network after an attack and can be used as a measure of the network's ability to resist extinction when facing destroyed.

$$R = N'/N \tag{8}$$

N represents the total number of nodes in the initial network, N′ represents the number of nodes in the maximum connected subgraph after it has been attacked.

2.4.6. Node pair removal approach

To further validate the initial hypothesis, this study conducted node pair removal experiments. We randomly combined 11 nodes in the food web in pairs, resulting in a total of 55 unique combinations. Each node pair was sequentially removed from the network. After removing a node pair, it was reintroduced into the network, and the next round of removals was carried out. Since network efficiency reflects the overall connectivity of the network and measures the efficiency of information transfer between different nodes (Mülken and Blumen, 2006), this study used network efficiency to indicate the changes in the robustness of the food web during the node pair removal process. The formula is as follows:

$$E = \frac{1}{n(n-1)} \sum_{ij} \frac{1}{d_{ij}^{w_{ij}}} \tag{9}$$

n represents the total number of nodes in the network, and $d_{(i,j)}$ represents the shortest path length between nodes i and j.

2.4.7. Statistical analysis

The carbon and nitrogen stable isotope values of various species were conducted to one-way ANOVA using SPSS 22.0, with a significance level of $p < 0.05$. Sequence and node pair removal experiments were conducted using Python 3.11.3. The food web model was constructed using MixSIAR in the R 4.1.2. Sampling point maps were created using ArcGIS 10.2. Graphs were plotted using Origin 2022 and CorelDRAW 2022.

3. Results

3.1. Trophic level characteristics of the main consumers in the food web

The stable isotope characteristics of each species in the food web can be seen in Fig. S2. Based on the nitrogen stable isotope results of each species, the trophic level characteristics of the main consumers were calculated, the results are shown in Fig. 1. In the typical food web of herbaceous marsh ecosystem in this study, the overall trophic level span of the consumers ranged from 1.81 to 3.29. Among them, the overall trophic level span of fish consumers was 2.05 to 3.29. The yellow catfish, as the top consumer, had the highest trophic level (3.29) in this study, followed by catfish with a trophic level of 2.98. Amur weatherfish and amur minnow had similar trophic levels (2.05). Zooplankton, as primary consumers, had a relatively high trophic level (2.47), which may be related to many complex factors and we will focus on this issue in subsequent studies. Aquatic insects had a lower trophic level of only 1.81.

3.2. Construction of the typical herbaceous marsh ecosystem food web model

The typical herbaceous marsh ecosystem food web model is shown in Fig. 2. The top predator, the yellow catfish, primarily fed on crucian carp (24.3 %). The contributions from the other five food sources were relatively even, with aquatic insects at 17.3 %, mudsnail at 15.8 %, amur sleeper at 15.6 %, and amur minnow at 15.2 %, amur weatherfish had a contribution of 11.8 %. In the diet of catfish, aquatic insects had the highest contribution at 28.0 %, followed by crucian carp at 22.3 %. In the diet of amur sleeper, amur minnow had the highest contribution at 62.4 %, followed by aquatic insects at 19.0 %. In the diet of amur weatherfish, amur minnow, aquatic insects, and mudsnail, aquatic plant also contributed the most, accounting for 69.4 %, 67.9 %, 73.5 %, and 73.4 % respectively.

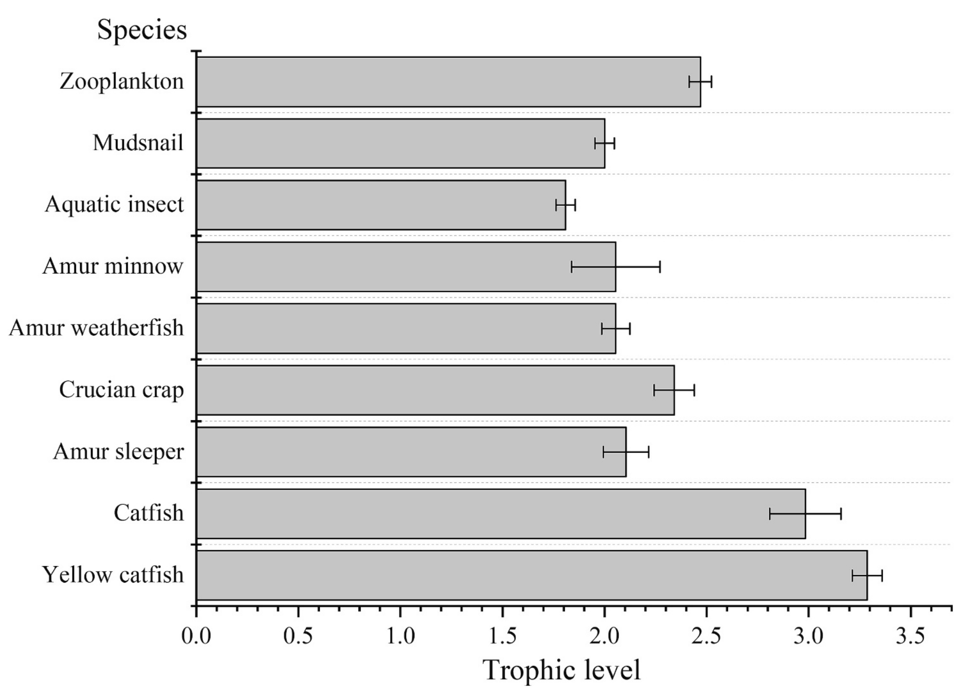

Fig. 1. Trophic level characteristics of the main consumers in the typical herbaceous marsh ecosystem food web (error bars are 95 % confidence intervals).

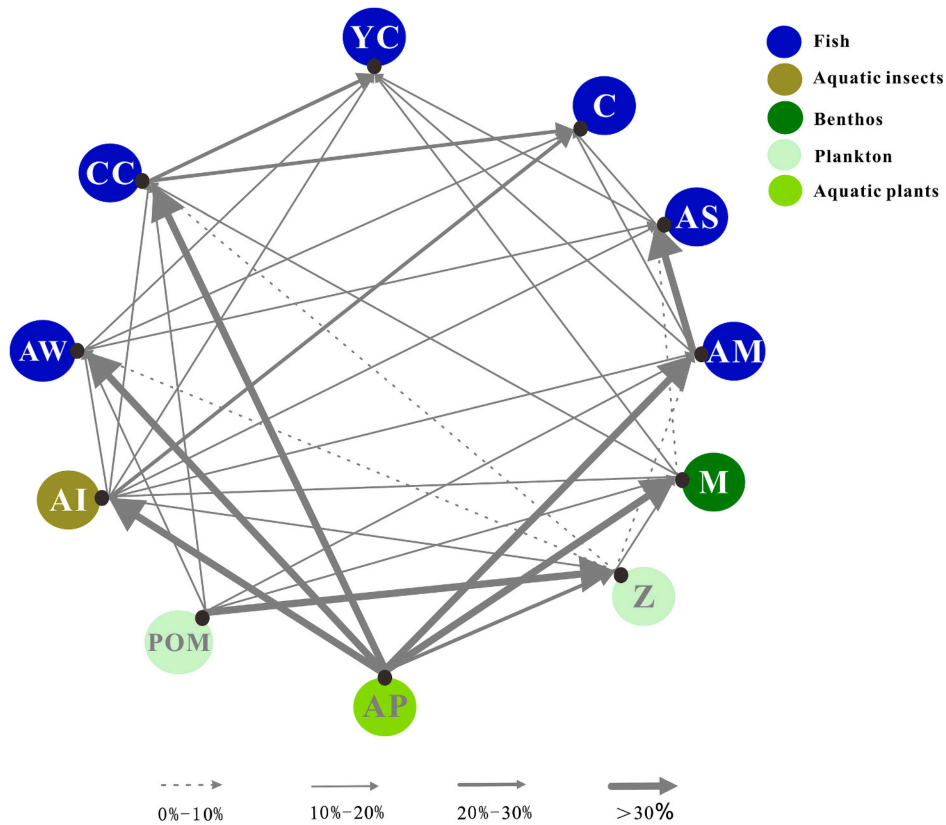

Fig. 2. The typical herbaceous marsh ecosystem food web model. (The line of different thickness represents the different feeding ratios between predators and their food sources. Different abbreviations represent "YC: yellow catfish; C: catfish; AS: amur sleeper; CC: crucian carp; AW: amur weatherfish; AM: amur minnow; AI: aquatic insects; M: mudsnail; Z: zooplankton; POM: particulate organic matter; AP: aquatic plant".)

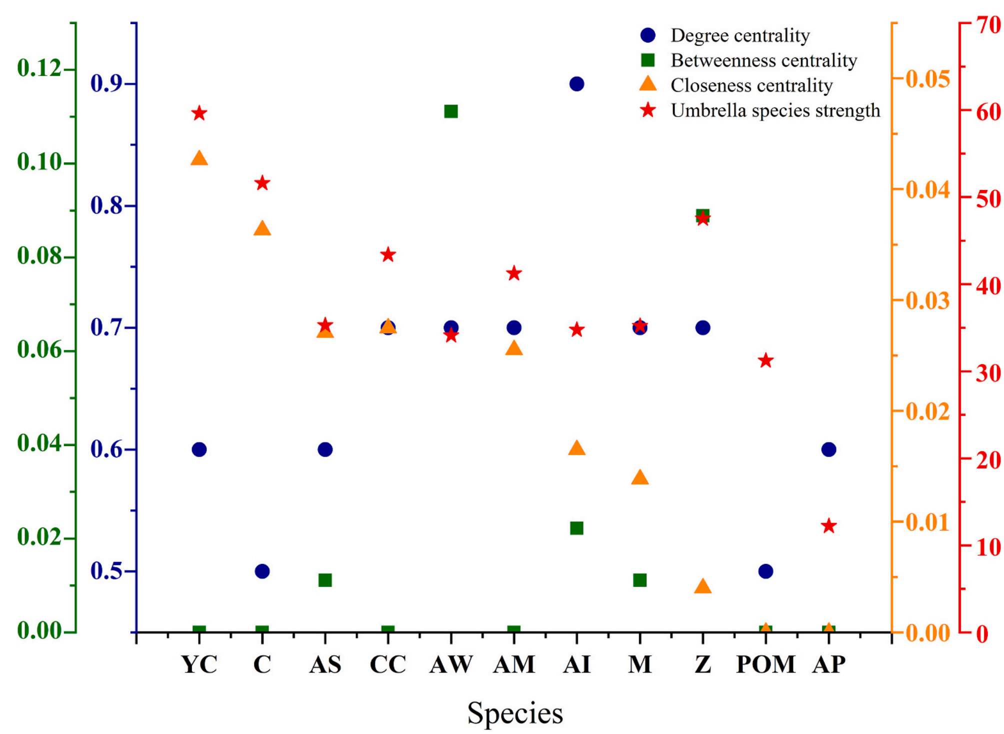

Fig. 3. Calculation results of centrality indices and umbrella species strength index of different species in the food web. (In the figure, different abbreviations represent "YC: yellow catfish; C: catfish; AS: amur sleeper; CC: crucian carp; AW: amur weatherfish; AM: amur minnow; AI: aquatic insects; M: mudsnail; Z: zooplankton; POM: particulate organic matter; AP: aquatic plant".)

3.3. Determination of keystone species and umbrella species in the typical food web in Honghe

The calculation results based on the centrality indices and the umbrella strength index are shown in Fig. 3. First of all, according to the results of umbrella species strength index, the umbrella species in the food web were determined. The results showed that the yellow catfish had the highest umbrella species strength index (59.600), followed by catfish (51.580). These two catfish species had significantly higher umbrella species strength compared to other species, making them suitable candidates as umbrella species in the typical herbaceous marsh ecosystem in Honghe.

Secondly, the degree centrality, betweenness centrality and closeness centrality of different species were calculated respectively, and based on this, different ranking results of the species importance were obtained. Aquatic insects had the highest degree centrality index (0.90), crucian carp, amur weatherfish, amur minnow, mudsnail and zooplankton had the same degree centrality of 0.7. From the results of betweenness centrality, amur weatherfish had the highest betweenness centrality (0.111), followed by zooplankton (0.089), and then aquatic insects (0.022). The top three in the ranking of species importance based on closeness centrality were yellow catfish (0.043), catfish (0.036), crucian carp (0.027).

Finally, from the above results, it can be seen that the results of the three centrality rankings are not the same. In order to find the most accurate method for determining the keystone species, this study continued to carry out the intentional removal and random removal experiments based on the calculation results of the three centrality indices, and observed the change of the relative size of the maximum connected subgraph indicating the robustness of the food web, the results can be shown in Fig. 4. The intentional removal based on the three centrality indices caused the food web to collapse more quickly compared with random removal. Under the intentional removal strategy, the relative size of the maximum connected subgraph was at its lowest when the node removal ratio reached 70 % (based on degree centrality), 80 % (based on betweenness centrality), 90 % (based on closeness centrality), which indicated that sequence removal based on degree centrality caused the food web to collapse the fastest. Species with a higher degree centrality are more influential, meaning that degree centrality is an effective indicator for determining keystone species. Therefore, based on results of degree centrality, we suggested aquatic insects as the keystone species in the typical herbaceous marsh ecosystem food web model.

3.4. Robustness analysis of the food web based on node pair removal

In the results of determining keystone species and umbrella species, we suggested aquatic insects as the keystone species, the yellow catfish and catfish are suitable candidates for umbrella species in the typical herbaceous marsh ecosystem food web model. And we continued to carry out the removal experiments of node pairs, which is also the most critical combination effect in this paper. Random combinations of 55 node pairs were created. Each time a pair of randomly combined nodes was removed, and observed the change in network efficiency, which reflects the information transmission efficiency between different nodes. The results are shown in Fig. 5. The initial efficiency of the food web was 0.236. Based on the network efficiency indicators for network robustness, when the “yellow catfish and aquatic insects” node pair was removed, the network efficiency decreased to 0.208. However, when the “catfish and aquatic insects” node pair was removed, the network efficiency reached its lowest point, at only 0.111. Based on this, although we suggest that the yellow catfish and catfish are suitable candidates for umbrella species in the above findings, we pay more attention to the combination effect. Numerical results of simulated removal experiments based on node pairs, we recommend “catfish (umbrella species) and aquatic insects (keystone species)” as the optimal combination of conservation management. These findings align with our initial hypothesis that the node pair of “keystone species plus umbrella species” has the most significant influence on the integrity and stability of the food web, making it the optimal combination for conservation management.

4. Discussion

In order to efficiently carry out species conservation and management, conservation biologists have attempted to incorporate surrogate species as representatives of broader species sets into conservation

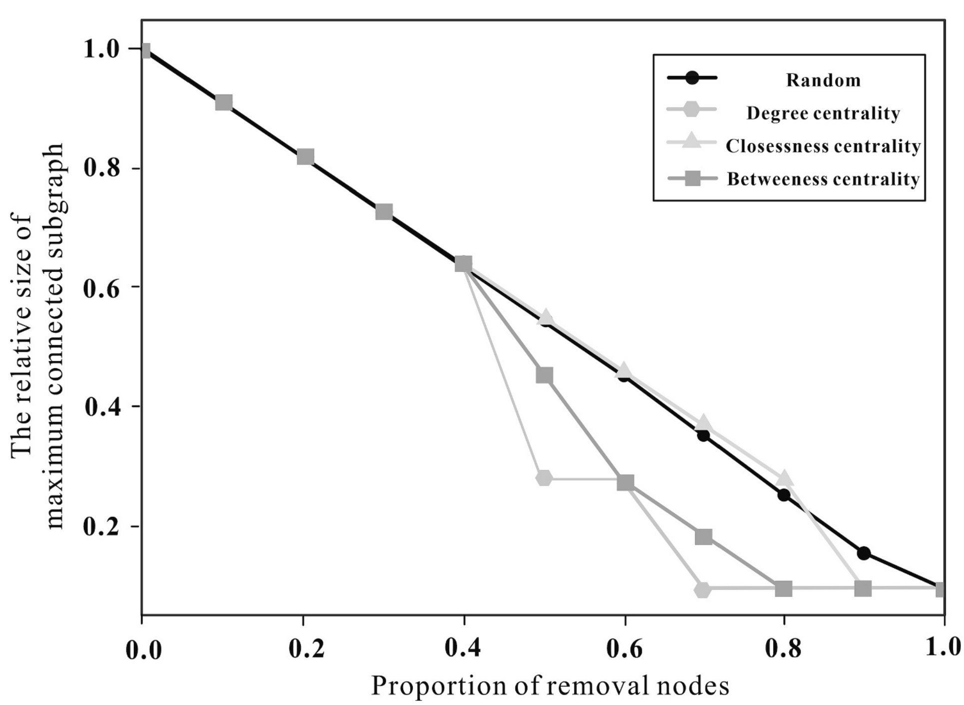

Fig. 4. The impact of topological sequence removal on the robustness of the food web.

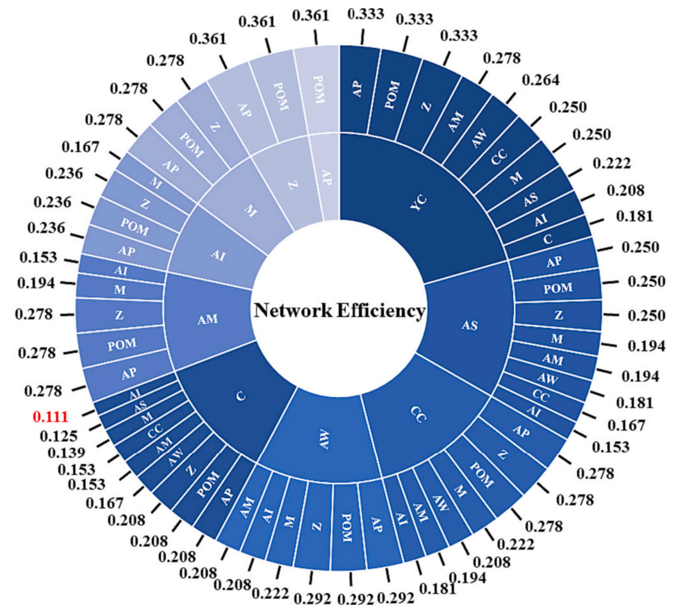

Fig. 5. The impact of removing different node pairs on the robustness of the food web. (The number in the figure represents the network efficiency when different node pairs are removed. The node pair highlighted in red in the figure is the "Catfish - Aquatic insects" node pair, which results in the lowest network efficiency when removed. Different abbreviations represent "YC: yellow catfish; C: catfish; AS: amur sleeper; CC: crucian carp; AW: amur weatherfish; AM: amur minnow; AI: aquatic insects; M: mudsnail; Z: zooplankton; POM: particulate organic matter; AP: aquatic plant".)

planning (Wiens et al., 2008). However, conservation efforts based on a single surrogate species often have limitations and biases due to different focal points (Roberge and Angelstam, 2004). To seek complementary and optimized management strategies, this study proposes the hypothesis that "keystone species plus umbrella species is the most suitable combination to reflect the integrity and stability of the food web" innovatively, and this hypothesis has been experimentally validated. The research findings can provide important references for improving the efficiency of biodiversity conservation and optimizing management decisions.

4.1. The protection of keystone species based on food web can help maintain the food web stability

Compared to other organisms in the ecosystem, keystone species play an overwhelmingly important role in maintaining the stability of the entire ecosystem (Sun et al., 2020). Network analysis based on centrality indices often provides valuable references for identifying keystone species (Wang et al., 2023; Santos et al., 2022). Unlike previous studies that commonly weight the links within food webs based on biomass or carbon flux data (Zhang et al., 2016), the different feeding ratios between predators and their food sources in the food web model constructed based on stable isotope data of each species is regarded as the link weight. By calculating the shortest paths between nodes and further evaluating the centrality indices of each node, the study accurately reflects the material transmission routes and the importance of each species in the real food web (Xing et al., 2021).

According to the results of this study, there are significant differences in the final ranking of species importance due to the different standards and evaluation perspectives of degree centrality, betweenness centrality, and closeness centrality (Xing et al., 2021; Luo, 2019). Node degree is a centrality measure that considers the direct influence of the nearest neighboring nodes on a local scale (Jordán et al., 2006; Estrada, 2007). Despite having a higher degree centrality due to more in-degree, the top predator, yellow catfish, is surpassed by aquatic insects that have more out-degree, making them the leaders in the ranking based on degree centrality in this study. Closeness centrality considers global network properties in the ranking of species in a network, and from this perspective, aquatic insects are considered to have a lower ability to spread network information. On the other hand, betweenness centrality aims to analyze the degree of influence in the exchange of information between species pairs, and in this study, species such as amur weatherfish, zooplankton, and aquatic insects in the intermediate layers of the food web have a higher control capacity for "communicating" in the network. In summary, these three centrality indices represent the positional importance of species at different scales, and these differences often indicate important structural differences between species, which will affect the structure, function, and stability of ecosystems in different ways (Estrada, 2007).

Stability is a multi-level concept that includes resistance, persistence, resilience, and robustness. Among them, robustness is commonly used to describe the ability of a system to resist extinction when faced with disturbances or attacks (Montoya et al., 2006; Simberloff et al., 2013) and is often used to investigate the loss of species (especially keystone species) and their impact on network stability (Allesina et al., 2009). Over the past few decades, the impact of random loss of nodes or selective removal of the most connected nodes on networks has been widely explored in interdisciplinary fields such as the Internet (Zhao et al., 2016). In this study, to further validate the effectiveness of centrality indices in determining keystone species, we compared the changes in network robustness when intentionally removing nodes and randomly removing nodes, and obtained consistent results with other studies that sequential removal based on centrality indices can cause the network to collapse faster compared to random removal (Sun et al., 2020; Wang and Tang, 2019), and degree centrality-based removal leads to the fastest network collapse. This indicates that degree centrality can successfully characterize the importance of species in ecological networks (Dunne et al., 2002), consistent with previous research findings (Albert et al., 2000). In a topological approach, species are considered extinct when they lose all their resources, and therefore, all secondary extinctions occur in cascades from the bottom up (EklöF and Ebenman, 2006). In addition, species with many binary links are unlikely to be isolated and therefore go extinct, so the node which is highly connected is often considered robust to species loss. In this study, aquatic insects (keystone species), which had the highest degree centrality, played a crucial role as hubs in the food web, they not only enriching the energy sources in the food web but also connecting the basal carbon sources with higher-level consumers. They made a substantial contribution to the food sources of higher trophic-level consumers, such as the yellow catfish and catfish, and played a crucial role in maintaining the stability of the food web. This finding is consistent not only with the habitat characteristics adjacent to the studied farm but also with the research results of Chen (2018) on the food web of the Sanjiang Plain wetland.

4.2. The protection of umbrella species based on food web can help maintain the food web integrity

Accurately determining umbrella species and managing the entire ecosystem by prioritizing the species with the highest conservation value have been acknowledged as crucial strategies for sustainable management, aiming to enhance the effectiveness of conservation efforts (Yang et al., 2023). Unlike previous studies that often used niche modeling or relied on community richness, abundance, and biomass surveys to determine and assess umbrella species (Maslo et al., 2016; Branton and Richardson, 2014), this study employed a food web approach to connect species with different spatial requirements. In this approach, every species within the food web was regarded as a co-occurring species that shares the typical herbaceous marsh habitat. Additionally, by incorporating the umbrella species strength index proposed by Li et al. (2023), which combines the essential concepts of degree, strength, and trophic level, the umbrella species were quantitatively identified. The results indicated that the yellow catfish and catfish were the most suitable umbrella species for the study area.

Choosing vertebrates, specifically fish, as umbrella species has been recognized as an effective shortcut for monitoring and managing freshwater biodiversity (Obester et al., 2022). It can assist conservation practitioners in making cost-effective decisions regarding freshwater protection (Itakura et al., 2020). In the context of this study, the selection of yellow catfish and catfish as the most suitable umbrella species candidates for the typical herbaceous marsh ecosystem is primarily based on the following reasons. Firstly, in terms of their feeding characteristics, yellow catfish is a typical omnivorous fish and catfish is a carnivorous fish. The results of the food web model in this study indicated that they preyed on aquatic insects and many fishes, exhibiting a relatively broad dietary range, indicating its greater ecological importance starting from the concept of degree centrality. As Barua (2011) pointed out, from a food web perspective, protecting umbrella species means safeguarding the species below them in the food chain. Secondly, trophic level is often considered a key discriminating factor in the process of determining umbrella species. Studies have shown that species occupying higher trophic positions have a greater impact on community structure (Sun et al., 2020; Berg et al., 2015). A meta-analysis based on study of top predators as an indicator of biodiversity has confirmed that top predators are reasonable candidates for biodiversity indicators (Natsukawa and Sergio, 2022). Therefore, top vertebrate predators are often seen as suitable candidates for umbrella species due to their wide home ranges (Li et al., 2023; Sergio et al., 2008). They can not only influence the entire food chain length through cascading effects in the ecosystem but also have significant roles in maintaining nutrient cycling, the integrity of food web functionality, and ecosystem stability (Xu et al., 2022). From the results of trophic level in this study, the two catfish species also conform to the characteristics of top predators.

In addition, in terms of ecological habits, both species inhabit freshwater areas with dense aquatic vegetation and slow-moving or stagnant water. The Honghe reserve preserves the largest marshland in China, characterized by herbaceous marsh vegetation and aquatic plants (Wu, 2019). The intact marsh ecosystem provides them with suitable habitats and spaces for survival and activities, resulting in their wide distribution. Yellow catfish is widespread in the eastern region of Asia, while catfish is distributed throughout the Eurasian continent. Meanwhile, as the concept of umbrella species is increasingly used to assist in delineating protected areas (Caro, 2003; Roberge and Angelstam, 2004), Seddon and Leech (2008) mentioned in their study that the criterion for selecting an umbrella species should indicate that it represents the area or habitat types. As typical species widely distributed in the typical herbaceous marsh ecosystem studied in this research, yellow catfish and catfish can well represent the characteristics of the typical herbaceous marsh ecosystem. Considering these factors, we believe that both yellow catfish and catfish, possess the qualifications as suitable umbrella species and can participate in conservation plans in the typical herbaceous marsh ecosystem. In the Honghe reserve, representing typical mid-high latitude herbaceous marsh wetland, we aim to leverage the positive conservation impacts of umbrella species to offer valuable insights and guidance to wetland ecosystem managers facing similar challenges (Branton and Richardson, 2014; Ozaki et al., 2006).

4.3. The management strategy of keystone species plus umbrella species as the optimal combination

Reducing a series of protected species to a more manageable set has been a management challenge for ecologists for decades (Wiens et al., 2008). Various attempts have been made to benefit a wider range of biodiversity. One approach is to use multiple flagship species as a conservation combination, referred to as "flagship fleets" (Veríssimo et al., 2014), or even a combination of multiple keystone species, known as a "keystone species complexes" (Hermosillo-Núñez et al., 2018). However, they still use the conservation concept of the same surrogate species to carry out biodiversity conservation. Conservation efforts relying on a single surrogate species often face limitations, which make it challenging to achieve comprehensive protection. Another approach is to assign multiple surrogate identities to a single species, integrating the functions of different surrogates, as demonstrated by the concept of flagship umbrella introduced by Caro (2010). Although this method integrates different conservation principles, the focus remains on the same species. Meurant et al. (2018) mentioned in their study that identifying more focal species would help improve more effective prioritization schemes, which can better match species ranking priorities (Roberge and Angelstam, 2004).

To address the limitations of previous studies and enhance conservation efficiency while minimizing costs, this study explores a management approach using combinations of two species. We validated our hypothesis through node-pair removal experiments. We found that when the node pair of yellow catfish (umbrella species) and aquatic insects (keystone species) was removed, network efficiency has decreased. Additionally, when the node pair of catfish (umbrella species) and aquatic insects (keystone species) was removed, the overall network connectivity reached its lowest point, indicating that the removal of this node pair had the greatest impact on the stability of the food web. Although the yellow catfish and catfish are both suitable candidate umbrella species, the number of links with other species in the food web and the shortest paths between them and other species in the food web are not the same, which is a key reason for the difference in results. According to the calculation results of network efficiency, "catfish and aquatic insects" is the optimal combination proposed by our study, and "yellow catfish and aquatic insects" is the sub-optimal combination, and we suggest that conservation managers should also use it as an alternative or useful reference. Overall, the result confirms our initial hypothesis and demonstrates the feasibility of the "umbrella species plus keystone species" conservation approach. Our study is based on the results of simulated sequential removal experiments and is expected to provide a reference for conservation priorities for biodiversity conservation actions. Previous research has shown that conservation actions based on keystone species often emphasize their fundamental role in maintaining the stability of the ecosystem, particularly in terms of food web stability (Sun et al., 2020). Conservation based on umbrella species revolves around the fundamental concept of offering umbrella protection to co-occurring species. Moreover, high trophic-level predators play a crucial role in maintaining the nutrient cycle and integrity of food web functionality (Xu et al., 2022). Hence, we can deduce that the combination management approach of keystone species plus umbrella species provides an effective solution to overcome the limitations of single surrogate species conservation. It enables comprehensive consideration and protection, taking into account the integrity and stability of the food web.

As Sumbh and Hof (2022) mentioned in their study, it is unrealistic to provide effective protection for all species in an ecosystem through a "one shoe fits all" conservation strategy based on the current conservation status. We agree with this statement. However, we can complement broader conservation strategies by adopting a multi-species combination management approach, thereby benefiting a greater number of species (Maslo et al., 2016). In this study, we focused on a typical herbaceous marsh ecosystem in northeastern China and constructed a food web model with fish as the top predator to quantitatively determine priority species based on the food web structure and network metrics. It is noteworthy that we innovatively proposed and experimentally validated our hypothesis, introducing for the first time the optimized management strategy of combining umbrella species and keystone species. We demonstrated how the effective combination of these two approaches can protect the integrity and stability of the food web, while considering the management of the entire ecosystem. The findings of this research aim to provide new insights for wetland ecosystem management, particularly for herbaceous marsh ecosystem, and offer valuable references to enhance the efficiency of biodiversity conservation efforts. For future research, we will also take this as a key entry point to carry out relevant research in more ecosystems. On the one hand, we will be committed to expanding the length of the food web and incorporating predatory species such as herons or raptors into the study of the food web. On the other hand, we hope to incorporate physiological, ecological, species habits and other variables into future research for more comprehensive consideration, and make more reasonable suggestions for conservation decision-making.

CRediT authorship contribution statement

Qiang Wang: Writing – original draft, Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Xingchun Li:** Writing – original draft, Methodology, Investigation, Writing – review & editing. **Xuehong Zhou:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110265.

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