



Effects of Urbanization on Amphibian Predation Networks in Kunming

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Abstract Urbanization is a significant driver of the loss of biodiversity and the disruption of ecosystems. Amphibians are especially vulnerable to the negative impact of urbanization as their life cycles and habitat requirements are complex. The present study investigated the effects of urbanization on amphibian predation networks in suburban Kunming in Yunnan, China and aimed to understand how predation network structure and stability vary with urbanization level. We constructed predation networks by analyzing the stomach contents of amphibians from 12 distinct urbanization gradients. We used the bipartite package in R to evaluate network robustness metrics such as modularity, nestedness, connectivity, and average shortest path length (ASPL). We found that urbanization level is negatively correlated with predation network connectivity ($R = -0.67$, $P = 0.02$), but there were no significant correlations between urbanization level and nestedness, modularity, or ASPL. Removal of the keystone species destabilized the predation networks at certain locations. The present work highlighted that maintaining prey quantity and diversity preserves predation network connectivity and stabilizes the overall network in urbanizing landscapes. It also underscored the critical role that keystone species play in sustaining network

robustness. The results of this research provided insights into the ecological consequences of urbanization. They also suggested that conservation measures should protect the key species and habitats of amphibian predation networks and mitigate the negative impact of urban development on them.

Keywords amphibian, network robustness, predation network, urbanization

1. Introduction

Urbanization is a primary driver of global ecological transformation. It significantly influences amphibian predation networks by contributing to habitat destruction, environmental pollution, and microclimate alteration (Bartley *et al.*, 2019; Zhang *et al.*, 2016). Urbanization fragments and diminishes the quality of the habitats within amphibian predation networks (Hamer *et al.*, 2008; Lescano *et al.*, 2018). It lowers the number of available natural amphibian habitats by replacing them with infrastructure such as buildings and roads. Furthermore, urbanization alters prey distribution and availability, thereby influencing amphibian foraging behavior and nutritional status. Water quality deterioration and chemical contamination caused by urbanization directly impact amphibian health and survival (Yletyinen *et al.*, 2016). Urbanization also disrupts amphibian reproduction and development by altering microclimates (Hamer and McDonnell, 2008).

Amphibians play a pivotal role in ecosystems. The stability of their predator-prey interactions is vital to overall ecosystem health (Bartley *et al.*, 2019; Dunne *et al.*, 2002; Giraldo *et al.*, 2024). The reductions in living space, shifts in prey distribution and availability, and environmental contamination resulting from urbanization directly affect amphibian health, survival, and reproduction and, therefore,

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alter predator-prey dynamics (Hamer *et al.*, 2008; Scheffers *et al.*, 2012). Environmental changes influence species predation patterns and, by extension, community robustness and resilience to species loss (Giraldo *et al.*, 2024). Robustness refers to the ability of a community to withstand species extinction. The connectivity, modularity, and nestedness influence the robustness of predation networks (Bartley *et al.*, 2019; Hastings *et al.*, 2016). Connectivity is defined as the ratio of observed to potential connections within a network. The average shortest path length (ASPL) is the mean shortest path between any two nodes on the network. In general, information transfer efficiency increases with decreasing average path length. Modularity identifies the tight and loose node connections within and between modules, respectively, and reflects network organizational structure (Gilaranz *et al.*, 2017; Olesen *et al.*, 2007). Theoretically, a high modularity buffers perturbations and enhances robustness in a network. Nestedness shows whether one module is contained within another.

Habitat fragmentation substantially lowers connectivity (Li *et al.*, 2022; Scheffers *et al.*, 2012). In fragmented landscapes, the isolation and altered size of the habitat patches may affect network structure (Li *et al.*, 2022). As specialized species tend to be more vulnerable than generalized species to habitat fragmentation, the former may disappear earlier than the latter from fragmented habitats. This loss subsequently disrupts the structure of ecological networks (Aizen *et al.*, 2012; Fortuna and Bascompte, 2006). Landscape fragmentation also lowers network robustness. In contrast, large habitat patches have relatively high interaction diversity, low species extinction risk, and, therefore, high network robustness (de Assis *et al.*, 2018; Emer *et al.*, 2020; Schleuning *et al.*, 2014; Valladares *et al.*, 2012). Fragmented environments are characterized by intense competition for prey, altered network connectivity, and niche expansion, creating new connections while blurring module boundaries (Whittaker *et al.*, 2017). Therefore, as urbanization intensifies, landscape fragmentation increases while the connectivity, modularity, nestedness, and robustness of amphibian predation networks decrease.

Urban traffic and waste management also disrupt predation networks (Alp and Cucherousset, 2018). Certain structural changes can significantly impact predation networks and, by extension, the survival of the species therein (Ebenman *et al.*, 2005). However, prior studies relying exclusively upon network topology failed to account for interactions and population dynamics (Xu *et al.*, 2020). Previous research on the effects of urbanization on amphibian population dynamics and genetic structure disclosed that urbanization levels are significantly negatively correlated with amphibian abundance (Yang *et al.*, 2022). When population dynamics are considered,

removing keystone populations can lead to secondary extinctions (Curtsdotter, 2011; Eklof *et al.*, 2006). Urbanization has multiple adverse effects on the robustness of the amphibian predation network. Habitat fragmentation reduces connectivity, thereby weakening network resilience to disturbances (Calderon *et al.*, 2019; Grass *et al.*, 2018; Hagen *et al.*, 2012; Liu *et al.*, 2023). It also destabilizes and lowers network biodiversity.

Here, we assessed the impact of urbanization-induced habitat fragmentation on amphibian predator networks. To this end, we used the landscape Shannon-Wiener diversity index (SHDI) to evaluate the effects of urbanization on amphibian predation network diversity, structure, and stability. We aimed to answer the following questions:

(1) Does urbanization-induced habitat fragmentation destabilize amphibian predation networks and lower species diversity in them? We examined the effects of urbanization on amphibian predation network connectivity, modularity, and nestedness as well as the potential implications of these characteristics for ecosystem stability.

(2) What is the impact of the urbanization-induced disappearance of keystone amphibians or other local species on predation networks?

2. Materials and Methods

2.1. Study site selection and urbanization-level calculations Kunming City is situated in the central part of the Yunnan Plateau. Its developed area is ~500 km² and encompasses the Wuhua, Panlong, Xishan, Guandu, Chenggong, and Jinning administrative districts. The unique geographical position of this region endows it with an indispensable strategic role in regional economic development. Moreover, the area is characterized by a rich diversity of amphibian species, making it an ideal location for investigating the effects of urbanization on amphibians. A 2 km × 2 km grid was overlaid using ArcGIS 10.8 (<https://community.esri.com/t5/esri-technical-support-blog/arcgis-10-2-released/ba-p/898164>). Land use classification data (10-m resolution) for China in 2020 were downloaded from the Finer Resolution Observation and Monitoring-Global Land Cover dataset (<http://data.ess.tsinghua.edu.cn/>). The proportions of impervious surface area in the grids were extracted and calculated to quantify the urbanization levels (Suarez-Rubio and Krenn, 2018). Based on the foregoing results, three sites with >30% coverage [Wanguan (WG), Guanshan (GS), and Xilin (XL)], five sites with 1%–30% coverage [Dewang (DW), Tianshengba (TSB), Huanglongqing (HLQ), Taoyuan (TY), and Laoyuhe (LYH)], and four sites with <1% coverage [Dongcun (DC), Shajinghe (SJH), Yaochong

(YC), and Shibadao (SBD)] were selected. The proportions of impervious surface area quantitatively indicate the physical effects of urbanization. The landscape SHDI is an ecological indicator of biodiversity and ecosystem health (Lei *et al.*, 2023; Kang *et al.*, 2019). Combining these metrics comprehensively assesses the impact of urbanization on ecosystems.

The proportion of impervious surfaces may not fully capture the changes in biodiversity. Thus, ArcMap 10.8 (<https://desktop.arcgis.com/en/arcmap/latest/get-started/setup/arcgis-desktop-system-requirements.htm>) and Fragstats 4.2 (<https://fragstats.software.informer.com/4.2/>) were utilized to calculate the landscape fragmentation SHDI within a 1-km buffer zone of the center of the study site and served as a proxy for the urbanization index.

2.2. Collection and identification of amphibian stomach contents A systematic survey was conducted at 12 sites between June 2021 and June 2023. Over three consecutive days, adult frogs were captured between 19:30 and 22:30 within transects 500 m long by 10 m wide, transported to a laboratory, and subjected to standardized emetic treatments (Solé *et al.*, 2005). Those deemed healthy post-treatment were returned to their original capture locations. The stomach contents were preserved in centrifuge tubes containing 75% (*v/v*) ethanol and examined and photographed under a Nikon SMZ1500 microscope (Nikon Corp., Shinagawa, Tokyo, Japan) fitted with a camera (Nikon DXM1200f). The amphibian species were identified by referring to the Color Map of Amphibians in China (Fei *et al.*, 2005, 2012). The insect prey species in the gastric contents were identified, and either their heads or other identifiable structures or organs were used for quantification (Wang *et al.*, 2020). The insect prey species were identified by referring to “Chinese Forest Insects” (Xiao *et al.*, 2020).

2.3. Construction of predation network Dietary data for the amphibians collected from the 12 sites were systematically gathered. The bipartite package in R 4.3.3 (<https://cran.r-project.org/web/packages/bipartite/index.html>) was used to plot a predation network based on the amphibian species and their insect prey categories. Network parameters, including links, nestedness, modularity, and ASPL, were quantified.

2.4. Data statistics

2.4.1. Analysis of the impact of urbanization on network robustness A regression analysis was conducted to (a) characterize the correlation between the SHDI and the predation network parameters, and (b) assess the impact of urbanization on amphibian predation network robustness. A regression analysis of the urbanization metrics against links,

nestedness, modularity, and ASPL was performed to establish the influence of urbanization on the predation network. The foregoing calculations were made in R 4.3.3.

2.4.2. Identification of the keystone species in the predation network A network topology analysis was conducted using the bipartite package in R 4.3.3 to determine the structure of the predation network and identify the important nodes and/or connections. To this end, nodes with high degree, closeness, and/or betweenness centrality were detected. Degree centrality is the number of connections between amphibians and their prey groups within the network, and was used to evaluate the robustness of the amphibian community network. The number of connections and the power of the nodes to stabilize the network increase with degree centrality. The degree centrality functions in Excel (Microsoft Corp., Redmond, WA, USA) were used to identify the keystone species in the Kunming urban amphibian predation network.

2.4.3. Assessment of the impact of species reduction on network dynamics The keystone and one randomly selected species were removed from the original predation network data, and the impact of their absence on network prey frequency was assessed. Random deletion was repeated for 100 iterations. An independent-samples *t*-test was performed in R 4.3.3 to compare the predation network before and after species deletion. Differences in insect prey frequency between the original and modified networks were quantified to identify keystone species and/or other community members significantly affecting network robustness.

2.5. Ethics statement All insect experiments were conducted in the Key Laboratory of Forest Disaster Warning and Control of Yunnan Province of Southwest Forestry University, and the Guidelines for the Management and Use of Laboratory Animals were observed. It was approved by the Academic Committee of Southwest Forestry University (SWFU-20250311).

3. Results

3.1. Collection and identification of stomach contents of amphibians in Kunming and suburbs We collected 804 stomach samples from 13 amphibian species. Output data included 3 373 and 62 prey records and prey categories, respectively. The most frequently recorded prey taxa included the Formicidae (492 occurrences), Labiduridae (378 occurrences), Carabidae (232 occurrences), and Melolonthidae (167 occurrences). Cicadellidae, Tipulidae, and Pentatomidae were observed 141, 119, and 89 times, respectively.

3.2. Relationship between urbanization index and predation network structure

The urbanization index reflects the degree of habitat fragmentation in environments with urbanized gradients. Here, GS and DC had the highest (1.66) and lowest (0.06) SHDI, respectively. We evaluated the interactions between species and the predation network by determining the average number of connections per species. We found that DW had the lowest mean number of connections (1.18), indicating that its predation network structure was relatively simple. Conversely, SJH had the highest mean number of connections (2.61) and, therefore, a more complex predation network structure. The nestedness index reflects the degree to which species are nested within the predation network. HLQ had the highest nestedness index (27.8), implying a strongly nested structure within its predation network. On the other hand, WG had the lowest nestedness index (16.3), suggesting only weak nesting in its predation network. Modularity reflects the degree of module division within a predation network. As TY had the highest modularity (0.39), its niche differentiation was strong. In contrast, WG had the lowest modularity (0.15) and, therefore, weak niche differentiation (Table 1).

3.3. Network robustness test The ASPL reflects the mean interaction distance between species within a predation network. The predation network in WG had the lowest ASPL (1.95), which indicates strong interconnectedness among species. However, LYH had the highest ASPL (2.39), suggesting weak interconnectedness among species (Table 1). Regression analyses showed that the urbanization index (SHDI) was negatively correlated only with the links ($R = -0.67$, $P = 0.02$) (Figure 1), while no significant correlations were found with nestedness, modularity, or ASPL. Thus, increasing urbanization leads to a decline in both network robustness and connectivity, while connectivity serves as a key

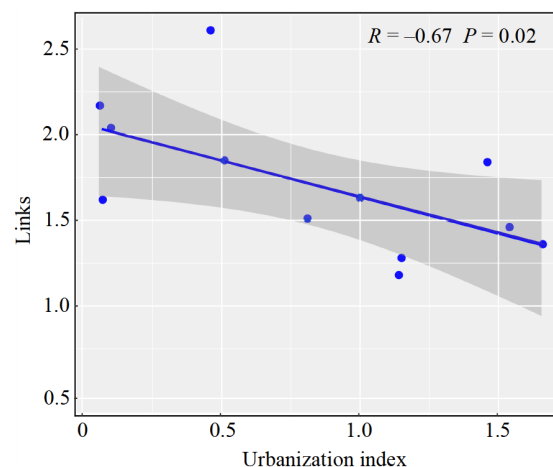


Figure 1 Equation and diagram representing urbanization and predation network structure.

indicator of network robustness.

3.4. Keystone species analysis Analysis of the predation network data revealed that Yunnan pond frogs (*Nidirana pleuraden*; short form: pond frog) had significantly more connections than other amphibian species with their insect prey groups. Bullfrogs had the second-highest number of connections with their insect prey groups, while *Glyphoglossus yunnanensis* had the lowest. Therefore, pond frog plays a vital role in the amphibian predation network of Kunming and is a keystone species in this ecosystem (Figure 2).

3.5. Network status before and after simulation The simulated elimination of 13 amphibian species altered the predation network of pond frog but had minimal impact on its overall complexity (Figure 3). Pond frog removal simplified the predation networks in YC, SBD, DW, and HLQ. Removal of the node for pond frog significantly altered the frequency of

Table 1 Relationships between the urbanization coefficients and the predation networks.

Serial No.	Site	Urb. index	Links	Nestedness	Modularity	ASPL
1	DC	0.06	2.17	23.9	0.36	2.22
2	YC	0.07	1.62	22.7	0.22	2.07
3	SJH	0.46	2.61	16.9	0.22	2.16
4	SBD	0.1	2.04	22.5	0.33	2.12
5	DW	1.14	1.18	20.9	0.26	2.18
6	HLQ	0.51	1.85	27.8	0.38	2.29
7	TSB	0.81	1.51	22.2	0.36	2.30
8	LYH	1.46	1.84	22.3	0.26	2.39
9	TY	1.00	1.63	18.5	0.39	2.11
10	WG	1.54	1.46	16.3	0.15	1.95
11	GS	1.66	1.36	22.9	0.28	2.24
12	XL	1.15	1.28	20.8	0.26	2.16

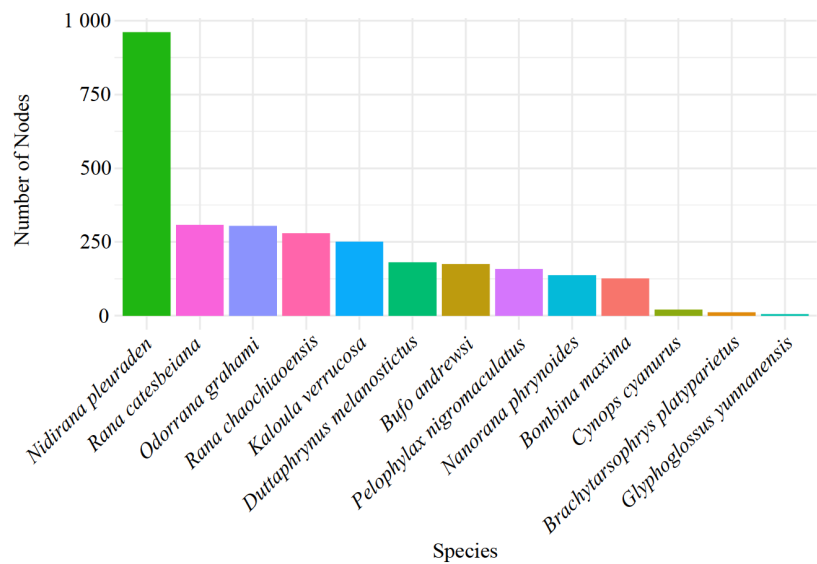


Figure 2 Amphibian predation network connections in Kunming, Yunnan, China.

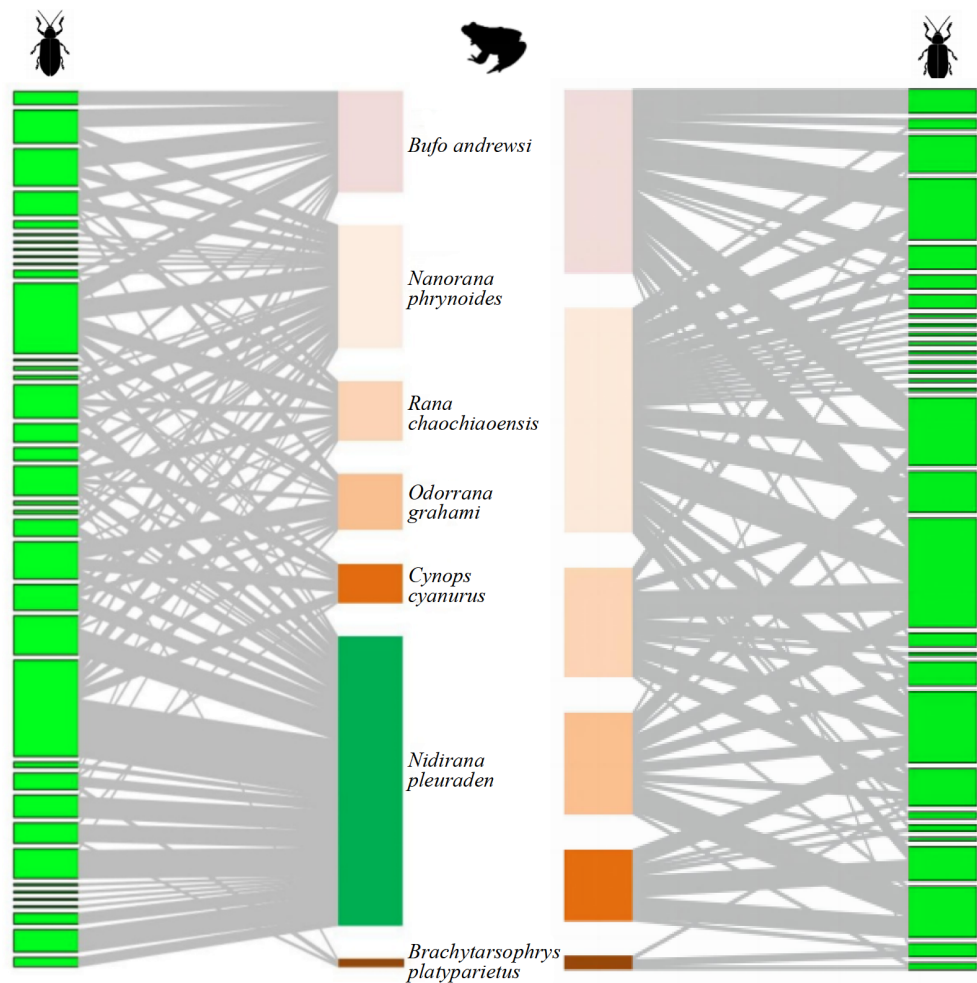


Figure 3 Status of the amphibian predation network in Shibadao (SBD) before and after the pond frog community reduction experiment.

predation interactions. The *t*-test results demonstrated significant decreases in the presence of pond frog in YC ($T = 2.46$, $P = 0.01$), SBD ($T = 2.15$, $P = 0.03$), DW ($T = 2.56$, $P = 0.01$), and HLQ ($T = 2.58$, $P = 0.01$) (Table 2). These sites were characterized by low urbanization levels and harbored large pond frog populations. Thus, as pond frog is a keystone species in this region, its disappearance could have a significant negative impact on the amphibian predation network there.

After random species deletion, the *t*-test of insect prey frequency was not statistically significant. Therefore, keystone species (here, pond frog), determining the characteristics of the amphibian predation network, had the highest nodal degrees. In contrast, the disappearance of species with comparatively lower nodal degrees had a weaker influence on the network characteristics. The effects of random species deletion on connectivity were 0.46 for *Rana chaochiaoensis* (SJH) and 0.01 for *Odorrana grahami* (DW) (Figure 4).

4. Discussion

4.1. Impact of urbanization on amphibian predation networks in Kunming This study examined the relationships between the urbanization index and amphibian predation network characteristics across an urbanization gradient in Kunming, Yunnan, China. There was a significant negative correlation between the urbanization index and network connectivity ($R = -0.68$, $P < 0.05$). Hence, predation network connectivity and network robustness decrease with increasing landscape diversity. Furthermore, landscape fragmentation reduces the number of effective species interactions and the resilience of the ecosystem to species extinction (Li *et al.*, 2022; Scheffers *et al.*, 2012). High urbanization reduces predation network connectivity, which,

in turn, destabilizes ecosystems. Moreover, rapid urbanization exacerbates these negative effects. The low numbers of connections in highly urbanized areas result in relatively simple predation network structures with few species interactions and the vulnerability of ecosystems to external disturbances. By contrast, a relatively low degree of urbanization is characterized by high connectivity, complex predation network structures, enhanced species diversity and interactions, and ecosystem stability and resilience (Calderon *et al.*, 2019).

Regression analyses of the nestedness, modularity, ASPL, and urbanization index were not statistically significant. In contrast, the performance indices of moderately urbanized areas were noteworthy. DW had the maximum nestedness (28.9). Hence, it had a pronounced nesting structure that favored community stability and species coexistence within its predation networks. As WG had a nestedness of only 16.3, its structural integrity was poor, and it was susceptible to environmental perturbations. As TY had the highest modularity, there was significant niche differentiation within its predation network, and its ecosystems had enhanced resistance to disturbances. Conversely, WG had low modularity, minimal niche differentiation, and reduced stability and was sensitive to changes in individual species. As it also had the lowest ASPL (1.95), it had close species interactions and efficient information and energy transfer, but increased susceptibility to species loss. On the other hand, LYH had the highest ASPL (2.39) and, therefore, dispersed interactions, high network resilience, and low energy transfer efficiency. The preceding observations reflect the strong influence of agricultural activity on moderately urbanized areas (Deknock *et al.*, 2020; Yang *et al.*, 2021).

Table 2 Results of the *t*-test of the amphibian prey simulation for Kunming.

Site	<i>df</i>	Pond frog deletion		Random species deletion	
		<i>T</i>	<i>P</i>	Mean <i>T</i>	Mean <i>P</i>
YC	1 021.5	2.46	0.01	0.16	0.733
DC	1 547.9	0.82	0.41	−0.04	0.644
SJH	1 527.3	−0.33	0.74	0.04	0.672
SBD	1 350.6	2.15	0.03	0.07	0.684
DW	1 018	2.56	0.01	−0.01	0.791
HLQ	1 012.1	2.58	0.01	0.08	0.770
TSB	1 526.3	1.24	0.22	0.01	0.719
LYH	1 544	0.62	0.54	−0.02	0.785
TY	1 359.4	1.56	0.12	0.05	0.777
WG	1 610	0.00	1.00	0.12	0.712
GS	1 540.3	0.37	0.71	0.03	0.746
XL	1 526.2	−0.18	0.86	0.09	0.724

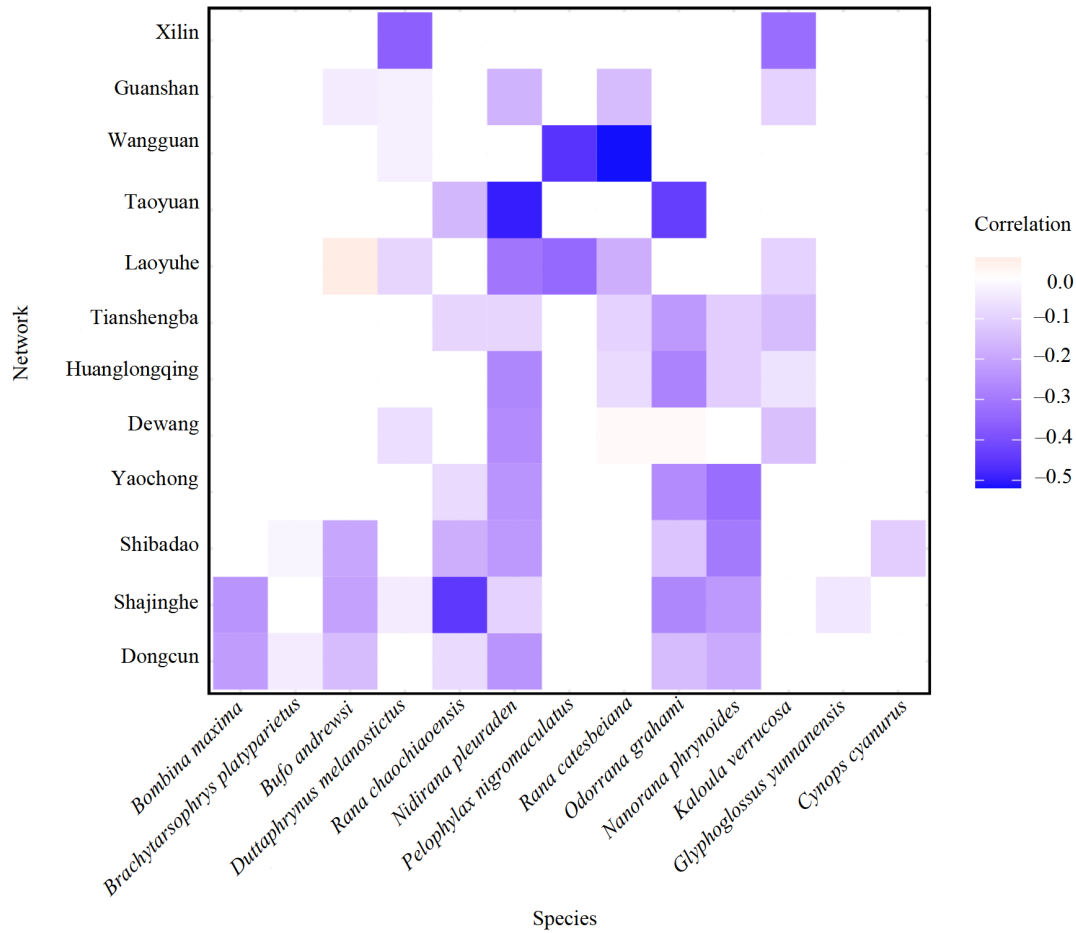


Figure 4 Degree to which the removal of a species diminishes the network connectivity.

4.2. Impact of keystone species disappearance on predation networks Keystone species help stabilize ecosystems and maintain their ecological balance (Curtisdotter *et al.*, 2011). The disappearance of keystone species from amphibian populations significantly alters the structure and function of predation networks (Eichenwald *et al.*, 2024). Though DC had high amphibian diversity, the extinction of the pond frog altered the predation network therein. Nevertheless, the overall complexity of the latter remained relatively stable in DC. In contrast, YC had relatively lower amphibian diversity, and the removal of the pond frog simplified the amphibian predator network therein. Thus, keystone species may contribute more significantly than non-keystone species to the robustness of predation network connections (Pongen *et al.*, 2024). Biodiversity is essential for ecosystem health as it increases and maintains the resilience of the ecosystem to environmental change. The loss of keystone species may reduce predation network robustness and, therefore, destabilize ecosystems. The disappearance of a keystone predator may lead to the overpopulation of its prey,

thereby adversely affecting the survival of other organisms and ultimately destabilizing the ecosystem. The impact of the removal of keystone predators at critical nodes in complex networks on dietary connectivity and function is controversial (Mishra, 2024). Here, we showed that the disappearance of the pond frog would significantly alter the predation frequency in the network. In low-diversity areas such as YC, the removal of keystone species would simplify prey chain structure and function.

The foregoing discrepancy implies that the loss of a keystone species may decrease robustness to a greater extent than the loss of a non-keystone species in a predation network (Eichenwald *et al.*, 2024). Biodiversity is intrinsically linked to ecosystem health as it strengthens resilience to environmental change (Bartley *et al.*, 2019; Dunne *et al.*, 2002; Giraldo *et al.*, 2024). The depletion of keystone species weakens both the adaptive capacity and the structural integrity of predation networks and may destabilize the ecosystem. The extinction of keystone predators regulating herbivore populations may result in the unchecked growth of certain plant species, affect

the survival of others, and destabilize the entire ecosystem. The loss of keystone species disrupts the internal ecological balance, compromises essential ecosystem services, and has significant socioeconomic repercussions. Therefore, strategies must be developed and implemented to safeguard keystone species. Habitat conservation, reintroduction programs, and ecological corridors require interdisciplinary collaboration and societal engagement (Deknock *et al.*, 2020; Steigerwald *et al.*, 2024). It is necessary to understand the extent to which the loss of a keystone species compromises the functions of an ecosystem so that its self-repair capacity may be restored through targeted interventions. Government policies and regulatory measures help safeguard keystone species and ecosystems. The formulation and implementation of effective environmental policies can help mitigate threats to keystone species and promote sustainable development. Long-term monitoring may assess the efficacy of conservation measures currently in place, and further research may help develop more effective ones. This integrated approach could effectively restore and conserve ecosystem health and stability.

5. Conclusions

Urbanization destabilizes and alters the connectivity of amphibian predation networks by reducing prey abundance and diversity. Studies on predation network dynamics demonstrated that the disappearance of the keystone species pond frog, significantly affects the predation networks in Kunming and its surrounding areas. Therefore, environmental conservation measures must be designed and implemented to ensure the protection of the pond frog and its habitat. Urbanization negatively impacts amphibian predation networks by depleting prey resources, destroying habitats, and degrading ecosystem services. Future research should explore the long-term effects of urbanization on amphibian predation networks and the implementation of ecological restoration and conservation measures as mitigation strategies. Protecting keystone species and enhancing ecosystem biodiversity should be integral parts of urban ecological planning and management.

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