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Seasonal population dynamics and dietary switching of *Vulpes* spp. amplify *Echinococcus* spp. transmission in the Eastern Tibetan plateau: implications for wildlife-mediated zoonotic risks

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Abstract

Background Echinococcosis, a severe zoonosis caused by *Echinococcus* spp., poses a significant public health challenge in the eastern Tibetan Plateau. This study aimed to investigate the interplay among seasonal shifts in definitive host ecology (*Vulpes ferrilata* and *V. vulpes*), dietary shifts, and infections with *E. multilocularis* and *E. shiquicus* within a high-altitude ecosystem.

Results Statistical analyses revealed that *V. ferrilata* dominated the local fox community (90.48%, $n=441$), with the highest number of samples collected in fall (46.49%), likely linked to dispersal behaviors after the breeding season. Dietary analysis showed a strong predation preference, with lagomorphs (primarily *Ochotona curzoniae*) accounting for 79.57% (74/93) of the diet. There was also a significant seasonal shift: among *Vulpes* spp., the consumption of rodents increased to 26.92% in the fall from being absent in the summer. This dietary diversification correlated with seasonal resource scarcity, driving foxes to exploit alternative prey. The infection rates of *Echinococcus* in *V. ferrilata* displayed the U-shaped seasonal patterns. Specifically, the infections of *E. multilocularis* peaked in the fall (12.29%), which was significantly higher than that in the spring (2.38%) and summer (0.74%), showing a positive correlation with the predation proportion on rodents ($R=0.61$, $P=0.036$). Meanwhile, *E. shiquicus* infections peaked in fall (29.32%) and dipped in summer (17.65%), but showed no dietary association, suggesting alternative transmission factors.

Conclusions These findings highlight that seasonal prey switching amplifies *E. multilocularis* transmission by increasing fox exposure to infected voles. The competitive pressure during resource-limited periods drives a

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shift in the predation strategies of the definitive hosts, inadvertently exacerbating the zoonotic risks of alveolar echinococcosis. The study underscores the importance of seasonally targeted interventions, providing a scientific foundation for alleviating echinococcosis in high-altitude regions under climate change pressures.

Keywords *Echinococcus*, Echinococcosis, Season, Host, Dietary, *Vulpes*

Background

Echinococcosis, a zoonotic disease caused by cestodes of the genus *Echinococcus*, represents one of the most complex and persistent public health challenges in both developed and developing countries [1]. Globally, it is estimated that over 1 million people are affected by cystic echinococcosis (CE) and alveolar echinococcosis (AE), the two primary clinical forms of the disease. The highest burdens are observed in pastoral and agro-pastoral regions of Central Asia, South America, East Africa, and the Tibetan Plateau [2]. Among the recognized species, *E. granulosus* sensu lato and *E. multilocularis* are the most clinically significant, being responsible for CE and AE, respectively, while *E. shiquicus*, a species endemic to the Tibetan Plateau, remains enigmatic in its zoonotic potential [3]. The Tibetan Plateau - spanning Qinghai, Sichuan, and Xizang - stands out as a global epicenter for echinococcosis, particularly AE, with an annual average incidence of 46.95 cases per million people, which is the highest in the world [4]. In Shiqu County, located in the eastern Tibetan Plateau, the incidence of AE reached a staggering 2,008.63 per million people per year [4]. This region's unique ecological and socio-economic conditions, including high-altitude ecosystems, extensive livestock grazing, and close human-wildlife interactions, create a perfect storm for sustained parasite transmission [5].

The life cycle of *Echinococcus* spp. hinges on a predator-prey dynamic involving definitive hosts (typically canids such as foxes, wolves, and domestic dogs) and intermediate hosts (small mammals like pika and voles, and ungulates like sheep and cattle) [6]. Adult tapeworms live in the intestines of definitive hosts, releasing eggs through feces into the environment. Intermediate hosts and humans become infected by accidentally ingesting these eggs, leading to the development of echinococcosis lesions in organs such as the liver and lungs. When definitive hosts consume infected intermediate hosts, the cycle is perpetuated [7]. This intricate interplay among hosts, parasites, and environmental factors is further modulated by seasonal variations in climate, resource availability, and host behavior [8]. For instance, temperature and humidity influence the survival of *Echinococcus* eggs in the environment [9], while seasonal variations in prey abundance drive shifts in predator dietary preferences [10].

Globally, the epidemiology of echinococcosis varies significantly across regions, being influenced by ecological, cultural, and economic factors [11]. Seasonality adds another layer of complexity [12]. Early studies found that the infection rate of *E. multilocularis* in the tundra voles (*Microtus oeconomus*) on St. Lawrence Island was less than 10% in fall but increased to 40% by early spring in the following year, continuing to rise and peaking in summer (80%) [13]. Meanwhile, the infection rate of *E. multilocularis* in the arctic foxes (*Vulpes lagopus*) on the island also showed seasonal fluctuations, with an annual average infection rate of about 77%. Specifically, by the end of May, only about 30% of individuals were infected, but this rate surges to nearly 100% by early fall [14]. In Switzerland, the infection rate of *E. multilocularis* in red foxes (*Vulpes vulpes*) around urban areas was significantly higher in winter (47.3%) than in summer (20.4%) [15]. In Hokkaido, Japan, the infection rate of *E. multilocularis* in *V. vulpes* showed a different seasonal pattern, with lower levels in spring, peaking in summer, dropping to a low in fall, and then rising again in winter [16]. The infection rate of the grey red-backed voles (*Myodes rufocanus*) in fall (8–12%) increased significantly due to the peak population density, while it dropped to 2–4% in spring [17].

However, the Tibetan Plateau, often referred to as the "Third Pole", presents a more complex situation. With an average elevation over 4,000 m, the region experiences extreme climatic conditions, such as sub-zero temperatures for most of the year, intense ultraviolet radiation, and a short growing season limited to summer [18]. These conditions shape a fragile ecosystem dominated by alpine meadows and sparse vegetation, where species such as the pika, vole and foxes play keystone roles. The plateau pika (*Ochotona curzoniae*), a small lagomorph, as well as the smokey vole (*Neodon fuscus*), a common rodent, serve as the primary intermediate hosts for *Echinococcus* spp., while the Tibetan fox (*V. ferrilata*) and red fox (*V. vulpes*) act as the dominant definitive hosts [3]. However, this system is not isolated; it intersects with human activities through livestock grazing, which brings domestic dogs - another critical definitive host - into contact with wildlife. This overlap creates a synanthropic cycle in which parasites circulate between wild and domestic hosts, amplifying zoonotic risks [19].

Despite decades of research, critical gaps persist in our understanding of the wild transmission cycles of *Echinococcus* spp. on the Tibetan Plateau. Most studies have focused on domestic dogs and livestock, overlooking the role of wildlife in maintaining parasite populations. For example, small mammals reduce surface activity

during winter, relying on underground burrows for survival, which may limit their exposure to *Echinococcus* eggs [20]. Conversely, in summer, pika and vole populations explode, providing abundant prey for foxes but also increasing the likelihood of parasite transmission [21]. Yet, how these seasonal patterns interact with host population dynamics, dietary shifts, and climatic extremes remains poorly quantified. This underscores the need to re-evaluate control strategies to address both domestic and sylvatic cycles.

This study aimed to bridge these gaps by examining the tripartite relationship between seasonal ecological changes, host behavior, and *Echinococcus* transmission in the eastern Tibetan Plateau. We hypothesized that seasonal fluctuations in definitive host abundance and dietary composition drive cyclical patterns in parasite prevalence, with cascading effects on human infection risks. To test this, we conducted a longitudinal survey in Shiqu County, Sichuan Province, collecting fecal samples from foxes across three seasons (spring, summer, and fall) in 2021. Molecular techniques were employed to identify host species, their dietary composition, and parasite infection status, while statistical models were used to explore correlations between ecological variables and infection rates.

Results

Host species composition and seasonal dynamics

The analysis of 685 collected fecal samples identified 441 as originating from foxes (Fig. 1 and Supplementary Table S1), with *Vulpes ferrilata* dominating at 90.48% (399 samples) and *V. vulpes* representing 9.52% (42 samples). Additionally, three, four, and one fecal samples were identified as originating from wolves (*Canis lupus*), Asian badgers (*Meles leucurus*), and Tibetan brown bears (*Ursus arctos pruinosus*), respectively. The remaining 236 fecal samples could not be attributed to any identifiable animal species. Seasonal sampling efforts showed significant fluctuations in host abundance and species composition (χ^2 = 10.58, *df* = 2, *P* = 0.005). Spring yielded the lowest number of samples (96, 21.77%), predominantly from *V. ferrilata* (87.50%, 84/96). By summer, sample numbers increased to 140 (31.74%), with *V. ferrilata* surging to 97.14% (136/140). Fall marked the peak collection period (205 samples, 46.49%), though the proportion of *V. ferrilata* declined slightly to 87.32% (179/205). The

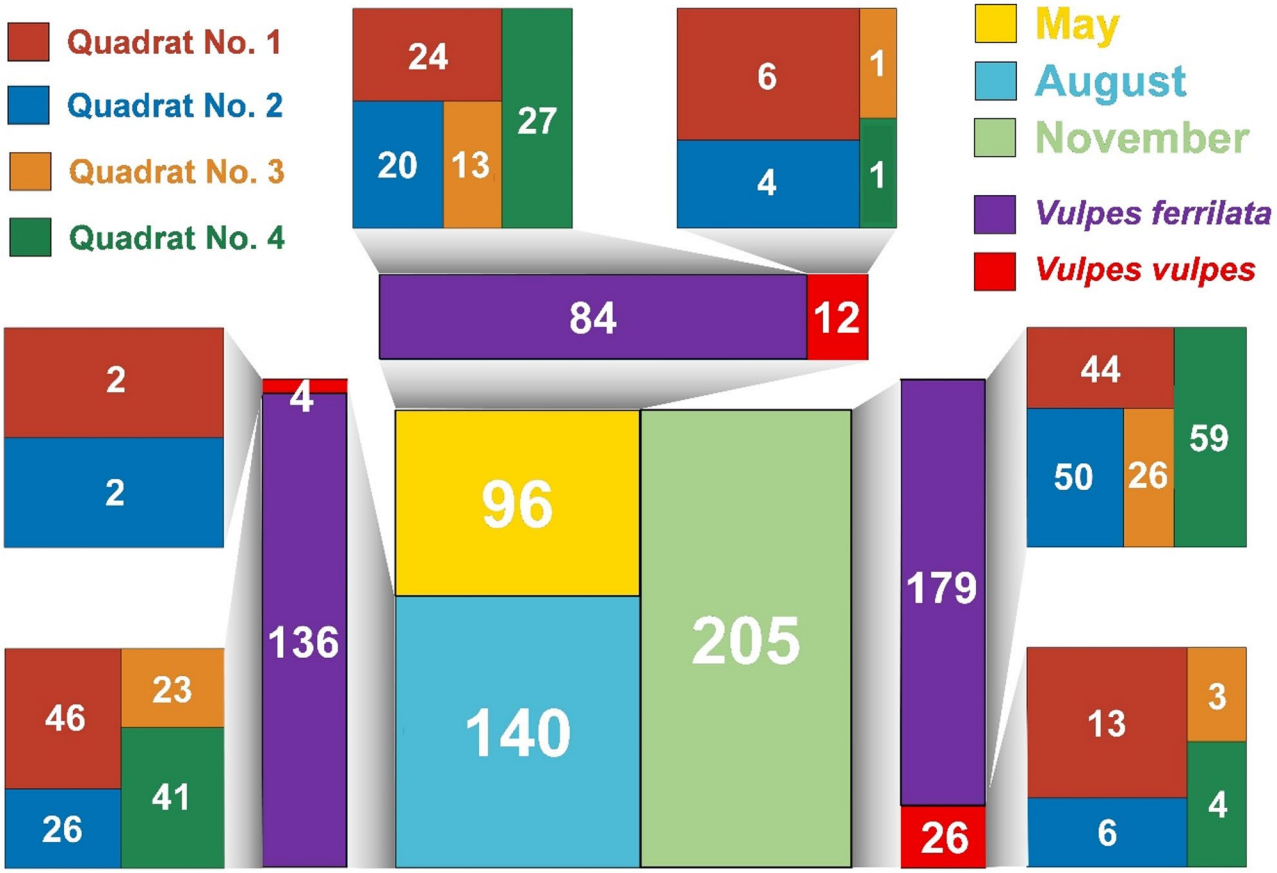

Fig. 1 Area proportion map of the *Vulpes* composition in different seasons and quadrats. The size of the rectangles represents the number of samples, and the numbers within the rectangles indicate the sample count

host species composition across quadrats highlighted niche partitioning (χ^2 = 11.98, df = 3, P = 0.007). *V. vulpes* activity was significantly higher in Quadrats 1 (15.56%, 21/135) and 2 (11.11%, 12/108), which were adjacent to human settlements, compared with remote Quadrat 4 (3.79%, 5/132), where *V. ferrilata* was dominant (96.21%). All *16s rRNA* gene sequence data of *V. ferrilata* and *V. vulpes* have been deposited in GenBank database under accession numbers PV414081–PV414175 and PV414176–PV414199, respectively.

Dietary composition and prey selection pattern

Dietary analysis of the 441 fox fecal samples detected DNA from small mammals in 93 samples (21.09%), with lagomorphs (Lagomorpha order) constituting 79.57% (74/93) of prey items, primarily *O. curzoniae* (76.34%). Rodents (Rodentia order), including mainly *N. fuscus* (11.83%) and lacustrine voles (*Alexandromys limnophilus*, 5.38%), accounted for 20.43% (19/93) of the prey DNA (Table 1). The dietary composition of foxes varied significantly among the three seasons (χ^2_{Yates} = 7.35, df = 2, P = 0.03), with the proportion of rodents in the diet increasing significantly in fall (26.92%, 14/52) compared with that in summer (no rodent detected). Dietary diversity, quantified via the Shannon-Wiener index, peaked in fall ($H = 0.67 \pm 0.41$ and 0.45 ± 0.26 at the species and order levels, respectively), reflecting adaptive foraging strategies under conditions of resource scarcity. Notably, no significant dietary differences were detected between *V. ferrilata* and *V. vulpes* (χ^2_{Yates} = 0.03, df = 1, P = 0.86), suggesting convergent predation strategies despite their spatial segregation. All *16s rRNA* gene sequence data of *O. curzoniae*, Gansu pika (*Ochotona cansus*), Moupin pika (*Ochotona* thibetana), *N. fuscus*, *A. limnophilus* and plateau zokor (*Eospalax bayleyi*) have been deposited in GenBank database under accession numbers PV413929–PV413955, PV414073, PV414201, PV414067–PV414071, PV414056–PV414060 and PV414064–PV414066, respectively.

Echinococcus detection rates and seasonal fluctuations

Molecular detection revealed an overall *Echinococcus* infection rate of 30.61% (135/441), with *E. shiquicus* at 28.34% (125/441), *E. multilocularis* at 7.48% (33/441), and co-infection at 5.22% (23/441). Host-specific detection rates differed significantly: *V. ferrilata* exhibited a higher *E. shiquicus* prevalence (29.32%, 117/399 vs. 6.27% for *E. multilocularis*), which was statistically significant (χ^2 = 72.51, df = 1, P < 0.0001); while *V. vulpes* showed comparable rates for both species (19.05%, 8/42). Seasonal U-shaped trends were pronounced for *E. multilocularis* of *V. ferrilata*, with infection rates rising from 2.38% (2/84) in spring to 12.29% (22/179) in fall, whereas *E. shiquicus* prevalence spiked sharply in fall (39.66%, 71/179) after a summer dip (17.65%, 24/136). The detection rate of *E. multilocularis* in *V. ferrilata* varied significantly across seasons (χ^2 = 20.30, df = 2, P < 0.0001), with the highest rate in fall (12.29%, 22/179) compared with spring (2.38%, 2/84) and summer (0.74%, 1/135). Similarly, the detection rate of *E. shiquicus* in *V. ferrilata* also varied significantly across seasons (χ^2 = 18.58, df = 2, P < 0.0001), with the highest rate in fall (39.66%, 71/179) compared with summer (17.65%, 24/136). In contrast, the detection rates of *E. multilocularis* and *E. shiquicus* in *V. vulpes* did not show significant seasonal differences (Table 2). All *cox1* gene sequence data of *E. multilocularis* and *E. shiquicus* have been deposited in GenBank database under accession numbers PV427030–PV427043 and PV427015–PV427029, respectively.

Interrelation among population, dietary and *Echinococcus* infection rates of foxes

Spearman correlation analysis showed a significant positive correlation between the detection rate of *E. multilocularis* in *Vulpes* spp. and the α diversity index based on dietary orders ($R_{Spearman}$ = 0.61, P = 0.036), indicating that an increase in the proportion of rodents (voles/zokor) in the diet of foxes was associated with an increase in the infection rate of *E. multilocularis* in *Vulpes* spp. Conversely, no significant correlation showed between the detection rate of *E. shiquicus* in *Vulpes* spp. and dietary composition. Additionally, the analysis demonstrated a significant positive relationship between the dietary diversity of foxes and the species diversity within their community ($R_{Spearman}$ = 0.67, P = 0.016). This pattern might reflect the generalist feeding strategy of *Vulpes* spp., whose broad trophic niche enables the exploitation of varied prey resources during periods of increased interspecific competition (increased proportions of *V. vulpes*), while simultaneously increasing contact with parasite-infected small mammalian populations (Fig. 2).

Discussion

Compared to large carnivores, small carnivores have lower individual space occupancy and larger population sizes, playing a more significant role in ecosystem stability and potentially acting as major reservoirs for pathogens [22]. As a unique ecosystem in the Tibetan Plateau, *Vulpes* spp. occupy a dominant position in the local carnivore community, which regulate the population structure of small mammals (primarily pika and voles) through predation and are also the primary definitive hosts for *Echinococcus* in the wild [5].

Seasonal dynamics of fox populations

In this study, the *Vulpes* population showed significant seasonal changes, increasing from spring to fall, along with corresponding changes in the species composition

Table 1 Dietary analysis of foxes (*Vulpes* spp.) in different seasons

Sampling months for each season	Quadrats (the number of fecal samples)[1]	Percentage of small mammal species detected from fecal samples (%)						Shannon Wiener indices based on small mammalian species (α_1) [*]	Shannon Wiener indices based on small mammalian orders (α_2) [#]
		Lagomorphs (Lagomorpha order)			Rodents (Rodentia order)				
		Pika			Voles		Zokor		
		Plateau pika (*Ochotona curzoniae*)	Gansu pika (*Ochotona cansus*)	Moupin pika (*Ochotona thibetana*)	Smokey vole (*Neodon fuscus*)	Lacustrine vole (*Alexandromys limnophilus*)	Plateau zokor (*Eospalax baileyi*)		
May	No. 1 (30)	10.00 (3/30)	0	0	10.00 (3/30)	0	0	0.69	0.69
	No. 2 (24)	29.17 (7/24)	0	0	8.33 (2/24)	0	0	0.53	0.53
	No. 3 (14)	28.57 (4/14)	7.14 (1/14)	0	0	0	0	0.50	0.00
	No. 4 (28)	7.14 (2/28)	0	0	0	0	0	0.00	0.00
	Total (96)	16.67 (16/96)	1.04 (1/96)	0	5.21 (5/96)	0	0	0.43 ± 0.26	0.31 ± 0.31
August	No. 1 (48)	9.52 (8/48)	0	2.08 (1/48)	0	0	0	0.35	0.00
	No. 2 (28)	17.86 (5/28)	0	0	0	0	0	0.00	0.00
	No. 3 (23)	8.70 (2/23)	0	0	0	0	0	0.00	0.00
	No. 4 (41)	7.32 (3/41)	0	0	0	0	0	0.00	0.00
	Total (140)	12.86 (18/140)	0	0.71 (1/140)	0	0	0	0.09 ± 0.15	0.00
November	No. 1 (57)	17.54 (10/57)	0	0	0	3.51 (2/57)	1.75 (1/57)	0.69	0.54
	No. 2 (56)	25.00 (14/56)	0	1.79 (1/56)	8.93 (5/56)	1.79 (1/56)	1.79 (1/56)	1.05	0.63
	No. 3 (29)	13.79 (4/29)	0	0	0	0	0	0.00	0.00
	No. 4 (63)	14.29 (9/63)	0	0	1.59 (1/63)	3.17 (2/63)	1.59 (1/63)	0.94	0.62
	Total (205)	18.05 (37/205)	0	0.49 (1/205)	2.93 (6/205)	2.44 (5/205)	1.46 (3/205)	0.67 ± 0.41	0.45 ± 0.26
Total		(71/441)	(1/441)	(2/441)	(11/441)	(5/441)	(3/441)	0.73	0.51

[1] As the results of the Chi-square test with Yates's correction for continuity ($\chi^2_{Yates} = 0.03$, $df = 1$, $P = 0.86$) showed no significant differences in the prey (food) compositions between *Vulpes ferrilata* and *Vulpes vulpes*, *Vulpes* species were not distinguished in this table

[*] Shannon Wiener indices based on small mammalian species was used to measure the food diversity for foxes with the formula $H_{species} = -\sum(P_i)*(\mathrm{Ln}P_i)$, where H represents the Shannon-Wiener Biodiversity Index, P_i represents the percentage of the species i number in the total number of all species, and Ln is the natural logarithm

[#] Shannon Wiener indices based on small mammalian orders was used to measure the diversity of food groups for foxes with the formula $H_{orders} = -[(P_{Lagomorpha})*(\mathrm{Ln}P_{Lagomorpha}) + (P_{Rodentia})*(\mathrm{Ln}P_{Rodentia})]$, where H represents the Shannon-Wiener Biodiversity Index, $P_{Lagomorpha}$ and $P_{Rodentia}$ represent the percentage of the Lagomorpha and Rodentia numbers in the total number of all orders, respectively; and Ln is the natural logarithm

of *V. ferrilata* and *V. vulpes*. These changes are closely related to the reproductive behavior, prey resource availability, and interspecific competition of *Vulpes*. Studies have shown that the mating season of *V. ferrilata* occurs around late February to early March, with a gestation period of about 50–60 days, with cubs usually being born in late April to early May. In the weeks following birth, the cubs remain in the den and cannot forage [23]. By summer, the cubs can follow the adults to hunt, which might explain the observed increase in the *Vulpes* population (Fig. 1). In fall, as the kits grow larger, they produce more feces, which are easier to collect. Additionally, as temperatures drop, the availability of prey on the ground decreases, forcing *Vulpes* to spend more time searching for prey in their habitats, which might also contribute to the higher number of fecal samples collected in fall [24]. Due to heavy snow cover in winter, no data were collected for this season. However, it can be inferred that the harsh winter conditions, with extremely scarce food resources and the lowest temperatures, may lead to the death of some *Vulpes*, resulting in a sharp decline in the *Vulpes* population by the following spring.

Furthermore, there is interspecific competition and niche differentiation between *V. ferrilata* and *V. vulpes*. Their spatial overlap is low, with *V. vulpes* having a wider range of activity than *V. ferrilata* (for example, in Quadrat 1 near human settlements, *V. vulpes* accounted for 15.56% of samples—four times higher than in remote Quadrat 4 of 3.79%). Their diurnal activity patterns also differ, with *V. ferrilata* being primarily diurnal and *V. vulpes* being more nocturnal [25]. The sharp increase in the *V. ferrilata* population in summer intensifies competition for food resources, forcing *V. vulpes* to leave their original habitats and forage for human food scraps. Although there is no definitive data to support this, our field observations during summer found a higher occurrence frequency of *V. vulpes* around human settlements compared to *V. ferrilata*, which might explain the lower proportion of *V. vulpes* feces in summer compared with that other seasons (Fig. 1). However, this overlap elevates the zoonotic risks of AE, emphasizing the need for waste management and community education to reduce human exposure.

Seasonal prey shifts of *Vulpes* spp

There was no significant difference in the proportion of lagomorphs and rodents between the diets of *V. ferrilata* and *V. vulpes*, however, they tended to prey more on pika (primarily *O. curzoniae*), because the larger size of pika provides a higher return (Table 1). Zheng, et al. found through high-throughput sequencing that the primary food resource for *V. ferrilata* is pika, followed by voles, as well as birds, some tailless amphibians, fish, and insects [26]. During the cold season (November to April of the following year), the dietary diversity and evenness of *V. ferrilata* were higher than in the warm season (May to October), but there was no seasonal difference in the intensity of predation on pika, which is consistent with the findings of this study. The seasonal differences in fox dietary composition reflect their adaptive predation strategies in response to ecological changes. In summer, small mammalian populations increase rapidly after the breeding period, providing abundant food resources for *Vulpes*, which preferentially prey on pika for more efficient energy return. However, in fall, the small mammal populations decrease due to predation and disease, and their surface activity decreases with falling temperatures, reducing the availability of food resources for *Vulpes*, forcing them to prey on all available alternative prey (such as voles, which are much smaller than pika), resulting in a U-shaped fluctuation in dietary diversity and the proportion of rodents [27]. Therefore, foxes exhibit unique adaptations to the Tibetan Plateau's extreme environment. Their ability to switch prey from pika to voles in fall buffers against seasonal food scarcity. This behavior might contribute to the more intense transmission of *E. multilocularis*.

Ecological mechanisms of *Echinococcus* infection seasonality

The U-shaped seasonal pattern of *Echinococcus* infections in *V. ferrilata* - peaking in fall for *E. multilocularis* (12.29%) and *E. shiquicus* (39.66%), and reaching lowest rates in summer at 0.74% and 17.65%, respectively (Table 2) - might be shaped by the interplay among host behavior, prey ecology, and environmental factors. In summer, a large number of *Vulpes* cubs without *Echinococcus* infection appear in the habitat, diluting the *Echinococcus* infection rate of the entire fox population. By fall, these cubs might begin to excrete eggs after preying on infected small mammals, leading to a continuous increase in the infection rate. In winter, infected individuals are more likely to die because of their declining physical condition [28], causing a decrease in the *Echinococcus* detection rate in fecal samples, which continues into the following spring. Additionally, Wang, et al. found that rodents are more susceptible to *E. multilocularis*, while lagomorphs are more susceptible to *E. shiquicus* [3]. Therefore, when the intensity of rodents predation by *Vulpes* decreases in summer, the infection rate of *E. multilocularis* in *Vulpes* might also decrease, which is consistent with the significant positive correlation between the detection rate of *E. multilocularis* in *Vulpes* and the proportion of rodents in their diet observed in this study (Fig. 2). Climate might further modulate these dynamics. For example, summer rainfall (>100 mm) prolongs *Echinococcus* egg survival in soil, while winter snow cover might protect the eggs from UV degradation [29], leading

Table 2 Detection rate of *Echinococcus* spp. In *Vulpes ferrilata* and *Vulpes vulpes* In different seasons

Hosts[1]	Sampling months for each season	Detection rate of Echinococcus (%) with 95% confidence interval						
		Echinococcus multilocularis		*Echinococcus shiquicus*		Mixed *E. multilocularis* & *E. shiquicus*		Total
		Rates	Chi-square (χ^2) tests[#]	Rates	χ^2 tests[#]	Rates	χ^2 tests[#]	
Tibetan fox (*Vulpes ferrilata*)	May	2.38 (2/84) [0–5.64] [a]	$\chi^2 = 20.30$, $df = 2$, $P < 0.0001$	26.19 (22/84) [16.79–35.59] [c, d]	$\chi^2 = 18.58$, $df = 2$, $P < 0.0001$	1.19 (1/84) [0–3.51] [e]	$\chi^2_{Fisher} = 16.92$, $df = 2$, $P = 0.0001$	27.38 (23/84) [17.84–36.92]
	Aug.	0.74 (1/135) [0–2.17] [a]		17.65 (24/136) [11.24–24.05] [c]		0.74 (1/136) [0–2.17] [e]		17.65 (24/136) [11.24–24.05]
	Nov.	12.29 (22/179) [7.48–17.10] [b]		39.66 (71/179) [32.50–46.83] [d]		10.06 (18/179) [5.65–14.46] [f]		41.90 (75/179) [34.67–49.13]
	Total	6.27 (25/399) [3.89–8.64]		29.32 (117/399) [24.86–33.79]		5.01 (20/399) [2.87–7.15]		30.58 (122/399) [26.06–35.10]
	χ^2 test[*]	$\chi^2 = 72.51$, $df = 1$, $P < 0.0001$						
Red fox (*Vulpes vulpes*)	May	8.33 (1/12) [0–23.97]	$\chi^2_{Fisher} = 2.08$, $df = 2$, $P = 0.40$	8.33 (1/12) [0–23.97]	$\chi^2_{Fisher} = 2.08$, $df = 2$, $P = 0.40$	0.00 (0/12)	$\chi^2_{Fisher} = 1.33$, $df = 2$, $P = 0.66$	16.67 (2/12) [0–37.75]
	Aug.	0.00 (0/4)		0.00 (0/4)		0.00 (0/4)		0.00 (0/4)
	Nov.	26.92 (7/26) [9.87–43.97]		26.92 (7/26) [9.87–43.97]		11.54 (3/26) [0–23.82]		42.31 (11/26) [23.32–61.30]
	Total	19.05 (8/42) [7.17–30.92]		19.05 (8/42) [7.17–30.92]		7.14 (3/42) [0–14.93]		30.95 (13/42) [16.97–44.93]
	χ^2 test[*]	$\chi^2 = 0.00$, $df = 1$, $P = 1.00$						
Total		7.48 (33/441) [5.03–9.94]		28.34 (125/441) [24.14–32.55]		5.22 (23/441) [3.14–7.29]		(135/441) [13.50–20.51]
χ^2 tests[∋]		$\chi^2_{Yates} = 7.22$, $df = 1$, $P = 0.007$		$\chi^2 = 1.98$, $df = 1$, $P = 0.207$		$\chi^2_{Yates} = 0.00$, $df = 1$, $P = 1.00$		

[1] As the results of Fisher's exact tests showed no significant differences in the detection of *E. multilocularis* and *E. shiquicus* among different quadrats (the result of $\chi^2_{Fisher} = 1.46$, $df = 3$, $P = 0.72$ for *V. ferrilata*; the result of $\chi^2_{Fisher} = 3.74$, $df = 3$, $P = 0.37$ for *V. vulpes*; and the result of $\chi^2_{Fisher} = 0.56$, $df = 3$, $P = 0.92$ for *Vulpes* spp. both *V. ferrilata* and *V. vulpes*), the specific data of the four quadrats were not listed in this table

[#] is a χ^2 test for the detection rate of *Echinococcus* sp. in *Vulpes* spp. among three different months

[*] is a χ^2 test for the detection rate between two *Echinococcus* species in *Vulpes* sp

[∋] is a χ^2 test for the detection rate of *Echinococcus* sp. between two *Vulpes* species

[a, b, c, d, e, f] represent results of the post-hoc tests of the χ^2 tests and Fisher's exact test for detection rates of *Echinococcus* spp. in different months; *P* values were adjusted by Bonferroni correction and compared with 0.05 level, the same letter indicates that there is no statistical significance between the two months. [a] and [b] only represent the test results of *E. multilocularis* detection rate in *V. ferrilata*. [c] and [d] only represent the test results of *E. shiquicus* detection rate in *V. ferrilata*. [e] and [f] only represent the test results of the mixed detection rate both *E. multilocularis* and *E. shiquicus* in *V. ferrilata*

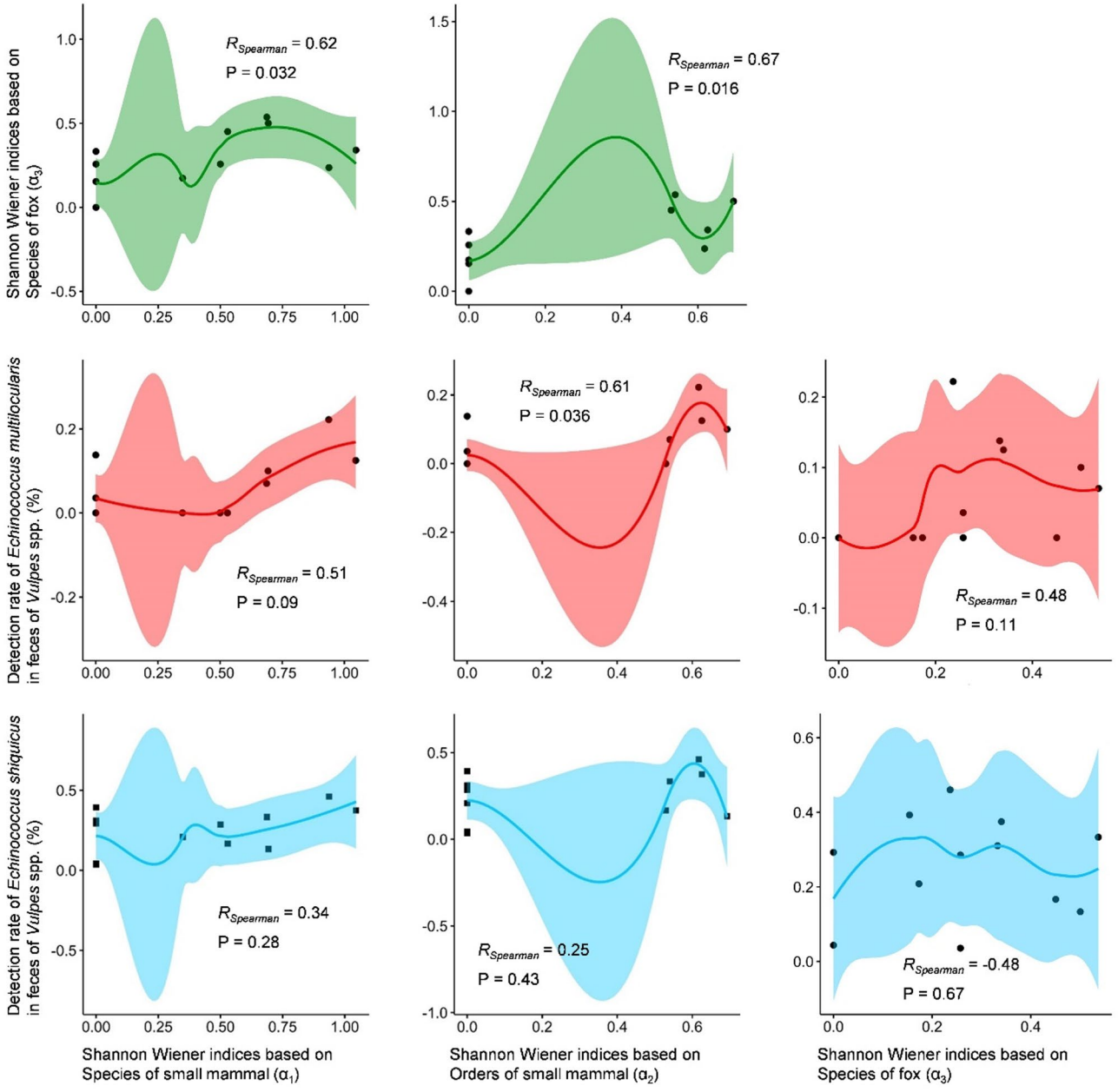

Fig. 2 Spearman correlation among population, dietary and *Echinococcus* infection rate in foxes

to egg enrichment in spring and fall, thereby increasing the rate of *Echinococcus* infection in the intermediate host and showing up in the definitive host through predation. In addition, host immunity might also play a role. Stress from winter resource scarcity could suppress foxes' immune function, increasing their susceptibility to infection. However, the nutrient intake in summer is sufficient to replenish the host's immunity [30].

Historical changes in *Echinococcus* prevalence

The results of this study show that *V. ferrilata* can be infected with both *Echinococcus* species, but with a significantly higher prevalence of *E. shiquicus*, while *V. vulpes* exhibits nearly equivalent infection rates for both *E. shiquicus* and *E. multilocularis* (Table 2). Previous studies have found that dogs in the same region can also be infected with both *Echinococcus* species, but are more susceptible to *E. multilocularis* [20]. However, earlier surveys conducted in 2012 indicated that the *V. ferrilata* had a considerably higher *E. multilocularis* infection rate (22.2%) than *E. shiquicus* (2.8%) at that time [31]. During this period, the Chinese government implemented a comprehensive echinococcosis control program at the end of 2014, strictly controlling the number of dogs,

especially stray dogs, in endemic areas. For example, most stray dogs were rounded up and adopted centrally, and a policy of no more than two dogs per household was gradually implemented, reducing the total number of dogs in Shiqu County from 56,658 to 14,443. Additionally, all domestic dogs were required to be leashed to prevent them from preying on wildlife, and a monthly deworming program for each dog was implemented to reduce *Echinococcus* infection rates in dogs [32]. By contrast, ecological conservation efforts in the Tibetan Plateau, such as the confiscation of hunting guns, strict control of the wildlife trade, and the establishment of national ecological parks (e.g., the Three-River-Source National Park), have been effective in stabilizing and recovering wildlife populations (e.g., foxes, wolves) [33]. These measures have led to a gradual reduction in the number of domestic dogs involved in the *Echinococcus* life cycle, while the population of wild animals, especially the dominant *V. ferrilata*, has increased. The foxes also likely gained more abundant pika prey resources due to the sharp decline in the dog population. These changes in definitive host populations and the potential alteration of their dietary structure ultimately led to a decrease in the prevalence of *E. multilocularis* and an increase in the prevalence of *E. shiquicus*. However, since no cases of *E. shiquicus* infection in humans have been reported, these control measures have significantly contributed to the protection of the local residents' health [34].

Thus, there are two *Echinococcus* transmission chains in the eastern Tibetan Plateau: one primarily involving *V. ferrilata* and *V. vulpes* as definitive hosts and lagomorphs (pika) as intermediate hosts for *E. shiquicus*, and another primarily involving dogs and *V. vulpes* as definitive hosts and rodents (voles) as intermediate hosts for *E. multilocularis*. Before 2015, due to the large population of dogs, the prevalence of *E. multilocularis* was similar to or even higher than that of *E. shiquicus*. However, after 2015, the number of dogs in the active transmission cycle decreased sharply, while the *V. ferrilata* population increased, leading to the dominance of *E. shiquicus* in the wild.

Limitations

This study only obtained one year of data, because the survey work in 2021 was followed by a series of echinococcosis control measures in the region, such as the release of praziquantel deworming baits and the launch of large-scale small mammal control operations. To ensure the reliability of the current data, the study was discontinued in this region. Thus the single-year sampling window limits our ability to assess interannual variability or long-term impacts, and the exclusion of winter data leaves critical gaps in understanding parasite survival under snow cover. Additionally, seasonal surveys of *Echinococcus* infection rates in small mammals corresponding to this study were lacking, because we aimed to minimize human interference in wildlife habitats to obtain more natural data. Finally, the focus on foxes overlooks potential contributions from other hosts, such as wolves (*Canis lupus*) or Eurasian lynx (*Lynx lynx*), which might participate in *Echinococcus* transmission [35, 36], despite their much lower population numbers compared with foxes. Nevertheless, this study provides a large amount of reliable data and appropriate theoretical exploration of wildlife population dynamics, dietary characteristics, parasite infections and their interconnections.

Conclusions

This study systematically analyzed the complex seasonal ecology among the population dynamics, dietary plasticity, and *Echinococcus* infection rates of *Vulpes* spp. in the eastern Tibetan Plateau. The study found that the transmission chain of *Echinococcus* in the region is significantly regulated by seasonal changes, with the shifts in the *Vulpes* population numbers and their predation intensity on small mammals jointly driving the peak of their *Echinococcus* infection rate in fall. Seasonal deworming of definitive hosts (e.g., deploying anthelmintic baits in the wild during autumn and winter, when fox populations peak and food resources are scarce, may enhance bait uptake and deworming efficacy) might be a feasible method to block the wild transmission chain of echinococcosis, providing a scientific basis for echinococcosis control in high-altitude regions. Ultimately, addressing echinococcosis requires a combination of One Health and EcoHealth approaches, harmonizing ecological preservation, public health, and community engagement in this fragile yet vital ecosystem [37].

Methods

Study area

The study was conducted in Yunbo Valley (33°11'N, 97°39'E), Sexu Town, west of Shiqu County, a high-altitude region situated on the southeastern margin of the Tibetan Plateau in Sichuan Province, China. Shiqu spans an average elevation of 4,520 m, with topographic features characterized by rolling alpine meadows (70% coverage), glacial valleys, and sporadic permafrost patches. The region lies within the Three-River-Source National Park, a protected area renowned for its biodiversity, including endemic species such as *V. ferrilata* and *O. curzoniae* [3].

Seasonal definitions

Seasonal divisions of the study area were based on temperature and precipitation thresholds validated against historical meteorological records (2000–2020): spring (March–May), with an average minimum

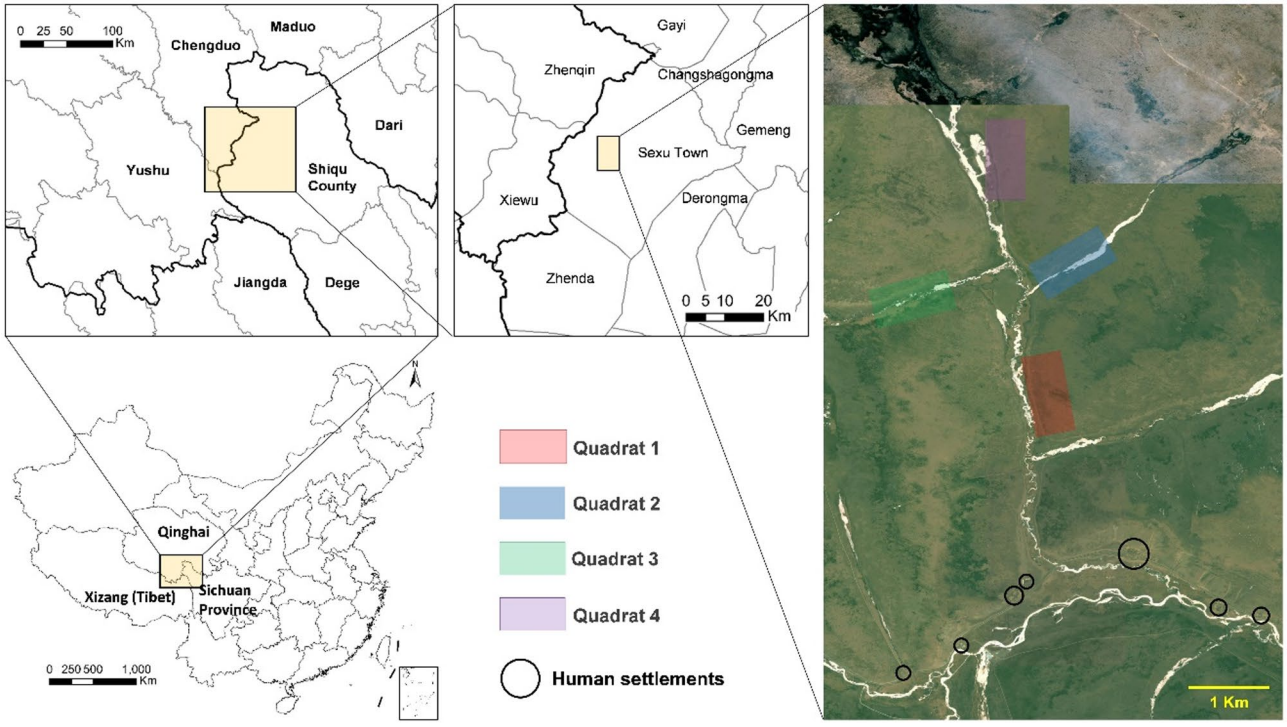

Fig. 3 Map of the quadrats setting

temperature < 0 °C, average precipitation > 10 mm, and partial snowmelt initiating vegetation green-up; summer (June–August), with an average minimum temperature > 0 °C, precipitation > 100 mm, peak plant biomass, and maximal small mammal activity; fall (September–November), with a mean daily minimum temperature < 0 °C, precipitation > 10 mm, vegetation senescence, and the onset of frost and snow; and winter (December–February of the following year), with an average maximum temperature < 0 °C and precipitation < 10 mm, and snow cover. Climate data were obtained from the China Meteorological Data Service Centre, National Meteorological Information Centre (https://data.cma.cn/).

Sample collection

In 2021, four 500 × 1,000 m quadrats were established in Yunbo Valley (Fig. 3). Carnivore fecal samples were collected by thoroughly searching the quadrats in late May (spring), August (summer), and November (fall). All samples were sourced from free-living wildlife, with none of the animals being privately owned by any institution, individual or farm. Due to persistent snow cover and logistical constraints snow cover, no samples were collected in winter. Sampling teams comprised three trained personnel, conducting surveys on each quadrate for 1 day from 10:00 to 15:00 in the late last month of each season. Collected fecal samples were first preserved in 50 mL tubes. A preliminary quality assessment was performed by the same investigator to discard weathered samples, retaining those with intact appearance, bright coloration, and appropriate density. Selected samples were preserved in 95% ethanol and transported to the laboratory for further processing. To avoid cross-contamination, disposable forceps were used for each sample.

Host and prey species identification

DNA was extracted from ethanol-preserved and − 80 °C inactivated fecal samples using the QIAamp DNA Stool Mini Kit (Qiagen, Hilden, Germany) numbered 51,604. PCR amplification was performed using universal vertebrate primers targeting the *16 S rRNA* gene sequence for the extracted DNA. The primer sequences were F/5′-GAGAAGACCCTATGGAGC-3′ and R/5′-ATAGAAACCGACCTGGAT-3′, with an annealing temperature of 55 °C, and a target product size of 380 bp [38]. The primers were synthesized by Sangon Biotech (Shanghai) Co., Ltd. (Shanghai, China). The reaction system consisted of 50 μL containing 24 μL ExTaq™ PCR Premix (2×) (which contains key components such as DNA polymerase, dNTPs, and buffer for the PCR reaction, providing the necessary material basis for amplification), 20 μL RNase-free Water, 1 μL bovine serum albumin (2%), 1.5 μL each of forward and reverse primers, and 2 μL template DNA. All PCR reagents were purchased from Takara Biomedical Technology (Beijing) Co., Ltd. (Beijing, China). PCR products were visualized by agarose gel electrophoresis, and positive products were sent to Sangon Biotech (Shanghai) Co., Ltd. for molecular cloning (10 clones

per sample) and sequencing. Host and prey species were identified by comparing the sequencing results with the NCBI database.

Molecular detection of *Echinococcus*

Nested PCR was performed on the extracted DNA using primers targeting the cytochrome c oxidase subunit I gene of *Echinococcus*. The first round amplification used the primers exF/5′-TTGAATTTGCCACGTTTGAATGC-3′ and exR/5′-GAACCTAACGACATAACATAATGA-3′, with an annealing temperature of 52 °C and a target product size of 874 bp [39]. The second round amplification used the primers Em-inF/5′-GTCATATTTGTTTAAGTATAAGTGG-3′ and Em-inR/5′-CACTCTTATTTACACTAGAATTAAG-3′ (annealing temperature of 52 °C, target product size of 243 bp) to amplify the *cox1* gene of *E. multilocularis*, and the primers Es-inF/5′-GTTGGTTACGTTACCGGTT-3′ and Es-inR/5′-TCTTATTAACATTTGAATTCAAC-3′ (annealing temperature of 52 °C, target product size of 420 bp) to amplify the *cox1* gene of *E. shiquicus* [40]. The amplified products were sequenced to identify the *Echinococcus* species in the fecal samples.

Statistical analysis

The number of fecal samples from foxes, the number of fecal samples with identified small mammalian species, and the number of fecal samples positive for *Echinococcus* were counted for each season and quadrat. Data were analyzed using SPSS 26.0 software(IBM Corp., Armonk, NY, USA), with appropriate statistical tests selected based on different conditions: Pearson's chi-square test (χ^2) was used when the expected count $T \geq 5$ and the total sample size $n \geq 40$; Yates's correction for continuity (χ^2_{Yates}) was used when the expected count $T < 5$ but $T \geq 1$ and the total sample size $n \geq 40$; Fisher's exact test (χ^2_{Fisher}) was used when the expected count $T < 1$ or the total sample size $n < 40$, or when the Pvalue was close to the significance level. Post-hoc pairwise comparisons were performed using Bonferroni correction, with a significance level of 0.05. Host species composition was analyzed using the Treemap tools in Hiplot Pro (https://hiplot.com.cn/), a comprehensive online platform for biomedical data analysis and visualization. The Shannon-Wiener indexes (α index) were calculated using the spaa package in R version 4.1.3, to quantify the dietary diversity of foxes and small mammals at the species and order levels (https://github.com/helixcn/spaa). Spearman correlation analysis was performed on the SRplot platform to examine the correlation between the fox dietary composition and *Echinococcus* detection rates, and loess regression curves were plotted [41].

Abbreviations

CE Cystic echinococcosis
AE Alveolar echinococcosis

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12917-025-04907-5.

Supplementary Material 1

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Author contributions

XW, YS and JC conceived the study. SH supervised the study. XW, CX, BL, YW, YK and SH investigated and collected samples from the field. XD, QC and CL completed the molecular detection. XW and QZ analyzed the result data. XW wrote draft of the manuscript. JY, SH, YS and JC revised the manuscript. All authors reviewed the article and approved submission.

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Data availability

The DNA sequences generated in the current study are available in the GenBank repository under accession numbers PV414081–PV414175, PV414176–PV414199, PV413929–PV413955, PV414073, PV414201, PV414067–PV414071, PV414056–PV414060, PV414064–PV414066, PV427030–PV427043 and PV427015–PV427029.

Declarations

Ethics approval and consent to participate

This study was performed in accordance with the Regulation on the Administration of Laboratory Animals (2013Revision). The research protocol has been approved by the Laboratory Animal Welfare & Ethics Committee of the National Institute of Parasitic Diseases at Chinese Center for Disease Control and Prevention (Chinese Center for Tropical Diseases Research) (approval number: IPD-2021-15).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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