



Prevalence of Tick Infection with *Bartonella* in China: A Review and Meta-analysis

Yuhua Wang¹ · Ruishan Li¹ · Ting Yin¹ · Zhen He¹ · Zhenhua Lu¹ · Zhongjun Shao¹ · Yong Long¹

Received: 13 February 2024 / Accepted: 30 July 2024
© The Author(s) 2024

Abstract

Objective Bartonellosis is a global vector-borne zoonosis caused by *Bartonella*, a genus of intracellular Gram-negative bacteria. It is one of 14 emerging infectious diseases that have recently been identified in China, and the prevalence varies by region. A more in-depth understanding is needed regarding the role and influencing factors of ticks in the transmission of *Bartonella*, including the infection rate of ticks with *Bartonella* in different regions. This study explored the prevalence of *Bartonella* in ticks and the factors that influence it.

Methods Databases (PubMed, Embase, Elsevier ScienceDirect, Cochrane Library, Web of Science, CNKI, VIP, CBM, and WanFang) were searched to review the preliminary research on *Bartonella*-carrying ticks in China.

Results We identified and included 22 articles. *Bartonella* infection rates in ticks varied from 0 to 22.79% examined by the included studies. Our meta-analysis revealed that the prevalence of *Bartonella* in ticks was 3.15% (95% CI: 1.22 – 5.82%); the prevalence was higher in parasitic ticks (4.90%; 95% CI: 1.39 -10.14%) than ticks seeking hosts (1.42%; 95% CI: 0.62 – 2.50%) ($P=0.047$).

Conclusion The prevalence of *Bartonella* in the southern region of China (6.45%) was higher than that in the northern region (1.28%) ($P=0.030$). Knowledge of ticks' vectors and reservoir competence is crucial to reduce the disease burden.

Keywords Ticks · *Bartonella spp.* · Tick-borne disease · Epidemiology · PCR · Prevalence

Introduction

Bartonellosis is a vector-borne zoonosis caused by the Gram-negative and facultative intracellular bacteria *Bartonella* (family Bartonellaceae, order Rhizobiales, class Alphaproteobacteria, and phylum Proteobacteria) [1] that can affect the health of both animals and humans [2]. All *Bartonella* species found in animals can cause infections in humans, emphasizing the zoonotic relevance of these bacteria. Blood-sucking arthropods (fleas, ticks, lice, etc.) are the main carriers of these bacteria, which colonize the endothelial and red blood cells of mammals, including carnivores, ruminants, rodents, and bats [3–5].

Bartonellosis is one of the 14 newly identified emerging infectious diseases in China; it has been detected in all provinces except Qinghai Province, the Ningxia Hui Autonomous Region, and Inner Mongolia Autonomous Region [6]. At least 13 *Bartonella* species are recognized for their ability to infect humans, leading to various diseases. Infection is common in both immunocompetent and immunocompromised patients [7]. *Bartonella* infections can incite inflammation and various complications, including Cat Scratch Disease (CSD), Oroya Fever, Peruvian Warts, Bacillary Angiomatosis, and Trench Fever. Three main pathogens - *Bartonella henselae* (*B. henselae*), *Bartonella quintana* (*B. quintana*), and *Bartonella bacilliformis* (*B. bacilliformis*) - are responsible for most infections. *Bartonella* is found in mammalian hosts worldwide, and it can be transmitted between hosts by hematophagous arthropod vectors or directly by infecting hosts [8]. *B. henselae* is primarily transmitted by fleas, *B. quintana* is mainly transmitted by lice, and *B. bacilliformis* is transmitted by sandflies. Although CSD is mainly transmitted by fleas, studies have shown that tick

✉ Yong Long
longyong@fmmu.edu.cn

¹ Department of Epidemiology, Ministry of Education Key Lab of Hazard Assessment and Control in Special Operational Environment, School of Public Health, Air Force Medical University, Xi'an, Shaanxi, China

exposure has been identified as a risk factor for human CSD [9, 10].

Ticks belong to the phylum Arthropoda, class Arachnida, subclass Acarina, order Parasitiformes, and superfamily Ixodida [11]. Hematophagous arthropods, such as ticks, are responsible for parasitizing vertebrates, including livestock, wild animals, and humans [12]. Ticks belong to three families, Argasidae, Ixodidae, and Nuttalliellidae, and the numerous species within these families exhibit considerable genetic diversity [13, 14]. Ticks transmit bacterial, parasitic, and viral pathogens and often carry multiple agents simultaneously. Tick-borne pathogens have a global presence with expanding ranges. The tick population is currently expanding. Furthermore, the geographical range and the number of suitable habitats of these arthropod vectors are increasing, accompanied by a proliferation in their associated pathogens [15]. Although research indicates that ticks and tick-borne illnesses are region-specific, they have the potential to occur worldwide because of the international movement of people, animals, and cargo from endemic to nonendemic regions [13]. According to the evidence, there has been a rise in the incidence of tick-borne diseases (TBD) worldwide. Studies have established *Bartonella* can be isolated and cultured from ticks, and Chang et al. confirmed the presence of human pathogens *Bartonella* in ticks [16].

The primary threat ticks pose to human and animal health stems from their pivotal role as vectors in the transmission of various pathogens; their epidemiological and epizootic significance ranks second only to mosquitoes [17–19]. The escalating prevalence and transmission of TBD represent significant public health concerns. Global attention has been drawn to the continuing geographical expansion of tick species, which could be influenced by climatic and environmental changes [20]. To control these emerging diseases, tick populations must be addressed, and the infections caused by the pathogens they carry must be identified and treated [21]. The globalization trend of ticks coupled with the increasing diversity of TBD underscores the need for in-depth research into the spatial distributions of both ticks and tick-borne pathogens, along with an exploration of their underlying risk factors. In recent years, scholars have been investigating ticks and TBD extensively because of the growing awareness of emerging tick-borne pathogens [22].

The current evidence indicates a global rise in the incidence of TBD; this necessitates a comprehensive understanding of the ecological niches occupied by major tick species and tick-borne pathogens to effectively monitor and control TBD [23]. This study investigated the presence of *Bartonella*-carrying ticks in China.

The surveillance of *Bartonella* in ticks is a valuable tool for assessing the risk of human exposure in susceptible populations.

Materials and Methods

Search Strategy

Following the formulation of an initial research question, a systematic search was conducted to identify pertinent publications. The following databases were searched to identify original studies addressing the detection of *Bartonella* in ticks: PubMed, Embase, Elsevier ScienceDirect, Cochrane Library, Web of Science, China National Knowledge Infrastructure (CNKI), China Science and Technology Journal Database (VIP), SinoMed (Chinese Biomedical Literature Database, CBM), and WanFang. The literature search involved the input of the specific terms in the title or keyword, abstract, and topic fields. The following keywords were utilized: bartonellosis, *Bartonella* infections, Cat Scratch Disease, Trench Fever, ticks, Ixodes, tick-borne diseases, prevalence, and China (detailed search strategies are documented in Table 1 in the Supplement).

After identifying potentially relevant articles, the studies were analyzed based on key characteristics, including the study setting, agent of interest, and study design. Original articles published between 1994 and 2023 were included. Title and abstract screening were performed using EndNote X9, and publications in Chinese and English were considered. Two authors independently reviewed all titles and abstracts and retrieved full-text articles if the screening suggested that they contained data on the prevalence of *Bartonella* in ticks. Data extraction was carried out and recorded in Excel (Microsoft Corporation, Redmond, WA, United States). The final study selection was determined through a thorough examination of titles, abstracts, and the full text, adhering to predefined inclusion and exclusion criteria. This meta-analysis ensures that a standardized approach is used to conduct and report on systematic reviews and meta-analyses.

Literature Screening and Quality Assessment

The following criteria were used to select eligible publications: (1) the study was performed on ticks; (2) ticks were collected from animals and/or the environment; (3) the detection method was polymerase chain reaction (PCR) or Real-time polymerase chain reaction (RT-PCR). After the selection process, an assessment of the data extracted

from the eligible studies to ensure quality. The following information was extracted: the lead author, year of publication, study area, sample size, number of cases, detection method, vector species, and the presence of other pathogenic agents. The following exclusion criteria were applied: (1) the study type was ineligible (systematic reviews or meta-analyses, case reports, guidelines, or recommendations); (2) the full-text article was not available; (3) the study did not include China; (4) the study was a duplicate (it was published in English and Chinese); (5) studies with fewer than 10 samples. Extracted data were checked by two reviewers. The AHQR (Agency for Healthcare Research and Quality) scale was used to evaluate the quality of the original literature.

Statistical Analysis

A meta-analysis of the data was conducted utilizing R 4.3.2 (Biostat, Englewood, NJ, USA). All tests were 2-tailed, and $P < 0.05$ was considered statistically significant. Nonparametric tests were employed to compare tick infestation rates across regions and ticks with different living habits. Studies exhibiting heterogeneity were analyzed using a random effects model. The forest plot provided a 95% confidence interval (CI), and publication bias was assessed with the Peters test and funnel charts.

Results

Summary of the Papers Used for the Meta-analysis

We identified 22 papers focusing on ticks infected with *Bartonella* to include in the meta-analysis. The study flow chart is presented in Fig. 1, and the comprehensive details of the studies included in this review are listed in Table 1. Of these publications, 6 are in English and 16 are in Chinese.

The geographic range of the tick samples in the included studies covered most of China, but most tick samples originated from Heilongjiang and Zhejiang Provinces. The sample size of the studies ranged from 24 to 1343 ticks. The tick species composition in each province is represented by pie charts, which show that the distribution of tick species differed between regions (Fig. 2). The ticks infected with *Bartonella* belonged to 14 species, the full list of species is presented in Fig. 2.

The random effect model was used for the meta-analysis because of the heterogeneity of the data in the included studies ($I^2 = 97.4\%$, Chi-square = 801.48, $df = 21$, and $P < 0.001$). The overall estimated prevalence of 3.15% (95% CI: 1.22 – 5.82%) (Fig. 3).

Comparison of Bartonella Infection Rates in Different Periods

The data extracted from the studies obtained from a comprehensive literature search were statistically analyzed to estimate the *Bartonella* infection rates in ticks, including the annual rates and trends of infection in China. The annual *Bartonella* infection rates in ticks ranged from 0 to 22.79% across the years examined by the included studies. Figure 4 presents the annual *Bartonella* infection trend in ticks in China. Notably, the infection trend did not discernibly decrease over time. Furthermore, statistical analysis revealed no significant difference in *Bartonella* infection rates in ticks over time (Kruskal-Wallis = 11.787, $df = 11$, $P = 0.38$).

Comparison of Bartonella Infection Rates in Ticks Collected from Animals vs. the Environment

We conducted a stratified meta-analysis to compare the *Bartonella* infection rate of ticks with different living habits. The heterogeneity analyses for animal-related rates and environmental rates yielded results of $I^2 = 98\%$ ($P < 0.01$) and $I^2 = 81\%$ ($P < 0.01$), respectively (Fig. 5). Consequently, we applied a random effects model for the meta-analysis. The findings revealed a prevalence of 4.90% (95% CI: 1.39 – 10.14%) in ticks collected from animals, whereas ticks collected from the environment exhibited a prevalence of 1.42% (95% CI: 0.62 – 2.50%). The difference between groups was statistically significant (Chi-square = 3.94, $P = 0.047$).

Comparison of Bartonella Infection Rates in Different Regions

We divided the studies into two groups according to region (south and north of China) and performed a stratified meta-analysis. The prevalence of *Bartonella* was 6.45% (95% CI: 1.74– 13.62%) in ticks collected from the south of China and 1.28% (95% CI: 0.60– 2.15%) in ticks collected from the north of China (Fig. 6). The difference between groups was statistically significant (Chi-square = 4.72, $P = 0.030$).

Publication Bias

We used the Peters test to assess bias. The test indicated that the included studies had a low likelihood of publication bias regarding the determination of *Bartonella* infection rates ($t = -0.73$, $df = 14$, $P = 0.479$) (Fig. 7). When studies were sequentially removed, the merged results of

Research on Identification through Database and Register

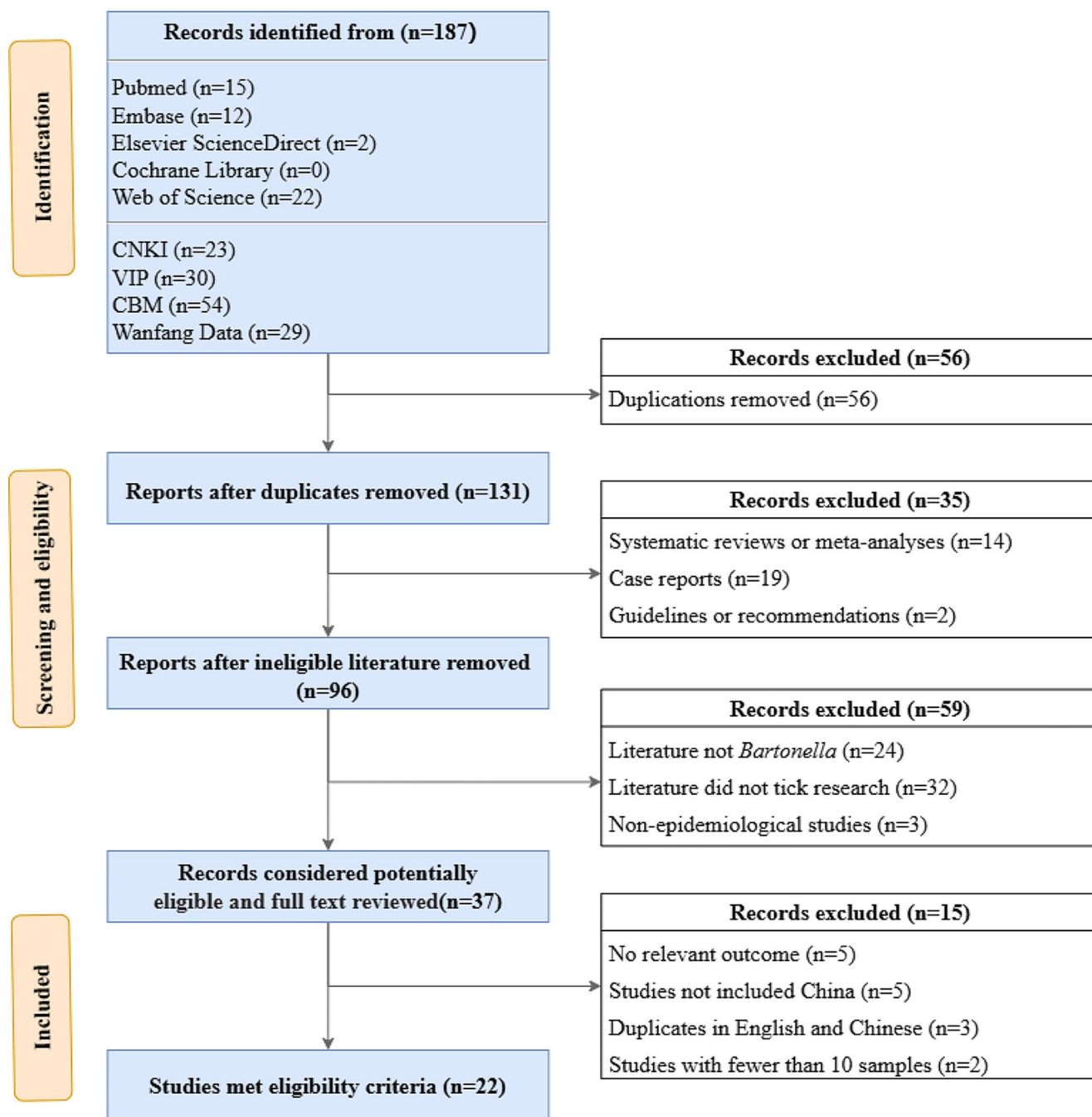


Fig. 1 Literature search and screening process

Table 1 Characteristics of *Bartonella*-infected ticks reported in the literature

region	group	IR (%)	Detection method	sampling		References
				<i>n</i>	date	
Southern	Animal	0.00%	PCR	47	2008–2009	[24]
Southern	Animal	16.28%	PCR	86	2005–2007	[6]
Southern	Animal	15.75%	PCR	254	2007–2009	[25]
Southern	Animal	9.96%	PCR	281	2008–2009	[26]
Northern	Environment	0.00%	RT-PCR	197	2011	[27]
Southern	Animal	0.00%	PCR	93	2012	[28]
Northern	Environment	3.19%	PCR	188	2014	[29]
Northern	Environment	0.00%	PCR	165	2013	[30]
Southern	Animal	2.30%	PCR	217	2012–2013	[31]
Northern	Animal	0.00%	PCR	24	2014–2015	[32]
Northern	Environment	1.20%	PCR	836	2012–2014	[33]
Northern	Environment	1.94%	PCR	257	2015	[34]
Southern	Animal	0.00%	PCR	500	2015–2016	[35]
Northern	Environment	3.44%	PCR	640	2012–2013	[36]
Northern	Environment	0.52%	PCR	388	2012–2014	[37]
Northern	Environment	3.35%	PCR	1343	2012–2014	[38]
Southern	Animal	2.40%	PCR	292	-	[39]
Southern	Animal	30.07%	PCR	818	2018	[40]
Southern	Animal	14.85%	PCR	330	2018	[41]
Northern	Environment	1.42%	PCR	351	2019–2021	[42]
Northern	Animal	0.86%	PCR	465	2020–2021	[43]
Northern	Animal	2.45%	PCR	163	2019	[44]

IR: Infection rate; PCR: polymerase chain reaction; RT-PCR: Real-time polymerase chain reaction

the remaining studies did not show significant changes, indicating a high robustness of the results (Fig. 8).

Discussion

This meta-analysis assessed *Bartonella* infection rates in China, revealing a prevalence of 3.15% (95% CI: 1.22–5.82%). TBD have garnered increased attention in the public health and veterinary medicine fields in recent years [45]. As arthropods, ticks can transmit a wider variety of pathogens than other vectors [46]. The presence of multiple co-infecting pathogens in ticks may contribute to the complexity of the disease [47]. Co-infection has been identified as a factor influencing the disease course [48]. Data on the vector competence of many tick species are limited, and the understanding of environmental factors affecting *Bartonella* transmission is insufficient. Thus, further studies are needed to evaluate relevant tick species and the factors that influence pathogen transmission.

We conducted a comparison of *Bartonella* infection rates in different regions, which revealed a prevalence of 6.45% in southern China and 1.28% in northern China. The main difference between the north and south of China lies in their climates; and climate change has the potential to impact both pathogens and vectors, influencing the survival and transmission of pathogens [49, 50]. Notably,

the tick life cycle is reliant on climate conditions, and tick-borne pathogens exhibit sensitivity to climate variations; factors such as temperature and humidity stress may impact pathogen transmission [51, 52]. Warming trends may enhance tick survival, shorten tick life cycles, increase larval hatch rates, and prolong the duration of the tick season. Climate change also has indirect effects on host communities, which could further contribute to the spread of tick-borne pathogens by altering tick populations [53–55]. Moreover, the distribution of tick species differs between the north and south of China, and these differences influence the ticks' pathogen-carrying capabilities. Most *Dermacentor* spp. and *Hyalomma* spp. are primarily distributed in the northern region, whereas they are uncommon in the southern region [56]. These variations significantly impact the regional *Bartonella* infection rates in ticks. Additional research is necessary to demonstrate the vector capacity of tick species [57]. Understanding vector competence and capacity is vital in predicting *Bartonella*'s expansion to new areas.

Our meta-analysis revealed a higher prevalence of *Bartonella* in ticks collected from animals (4.90%; 95% CI: 1.39–10.14%) than in ticks collected from the environment (1.42%, 95% CI: 0.62–2.50%). Because studies collect ticks from different hosts, the detected microbial DNA may not originate solely from ticks. Rather, it may be derived from blood powder, potentially originating

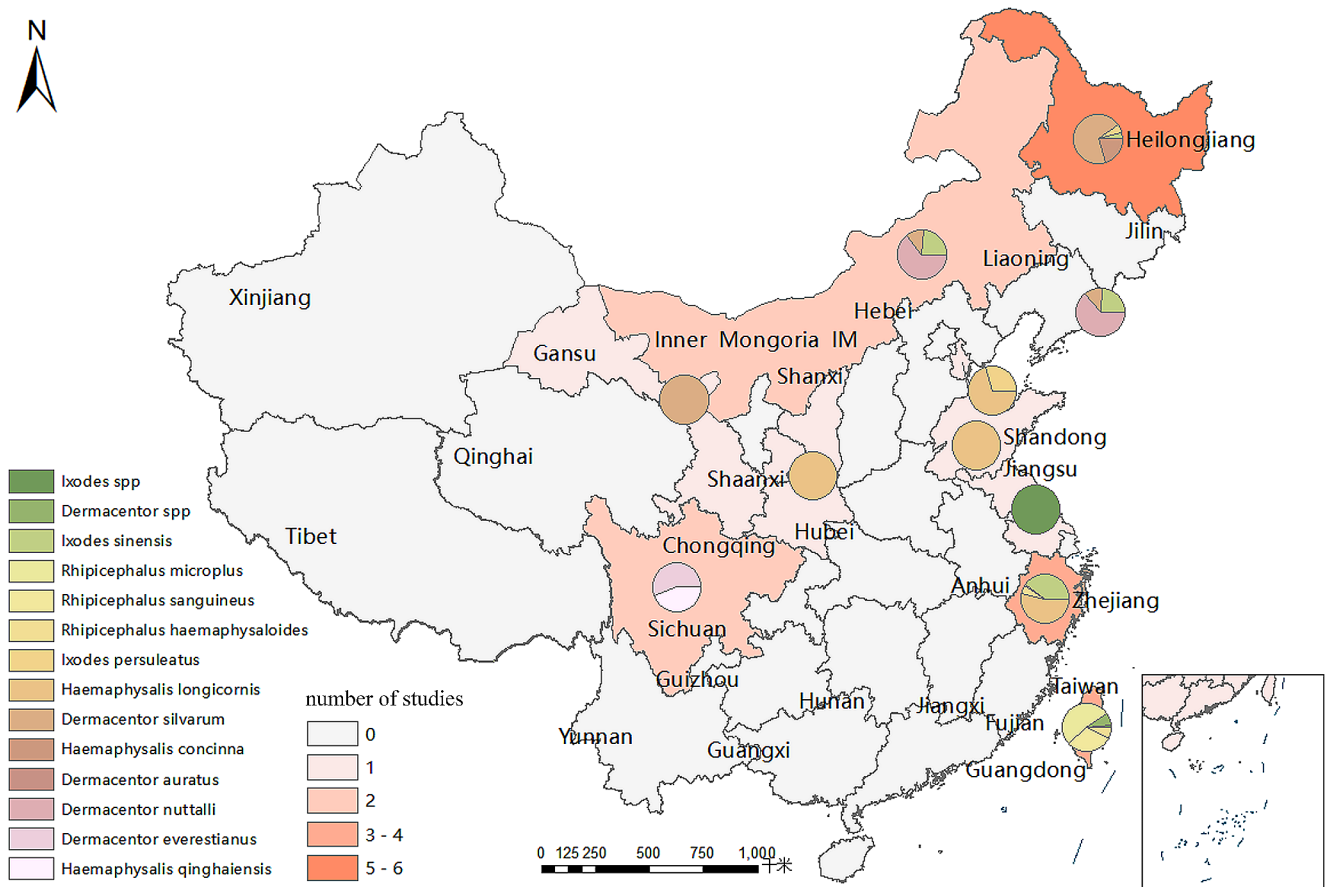


Fig. 2 Geographic distribution of tick samples across the included studies

from the host. Simultaneous feeding ticks can amplify the transmission of pathogens between ticks, a phenomenon more likely to occur in ticks collected from animals than in those collected from the environment [58, 59]. After a tick is infected with one bacterium, it has an increased likelihood of being infected with another bacterium [60]. Ticks that are gathered from the surroundings have a reduced rate of carrying pathogens because they are unable to sustain the normal transmission of pathogens without hosts [61]. Additionally, the bacterial richness of all ticks significantly decreases after they become engorged [62].

The *Bartonella* infection rate is also influenced by the tick species; various studies have suggested that tick species impact bacterial diversity [63, 64]. A previous study indicated that the infection rate of *Dermacentor everestianus* (*D. everestianus*) was higher than that of other tick species. *D. everestianus* is predominantly distributed in Tibet, China, and is well-adapted to highland areas [65]. *Haemaphysalis qinghaiensis* (*H. qinghaiensis*) is particularly prevalent in Qinghai, Gansu, Sichuan, and Tibet Provinces [66]. By contrast, *Haemaphysalis longicornis* (*H. longicornis*) transmits the largest number of

pathogens of all tick species, including Dabie bandavirus, tick-borne encephalitis virus, *Borrelia burgdorferi*, *Anaplasma phagocytophilum*, and *Babesia*, among others [67, 68]. The distribution of *Dermacentor silvarum* (*D. silvarum*) spans from 22°N to 57°N and has been widely reported in northern China [69]. The distribution of *D. silvarum* is concentrated in areas with boreal climates featuring precipitation and boreal winter dry climates [70].

Detecting subtypes of pathogens with pathogenic potential in humans facilitates a more precise assessment of human disease risk [71]. The impact of Bartonellosis on animals and public health varies based on the *Bartonella* species, infection stage, immune characteristics, and geographical area [72]. CSD was initially described in 1931 and is the most common syndrome associated with *Bartonella* infection [73]. CSD, caused by *B. henselae*, is typically characterized as febrile lymphadenopathy, which is also among the most common venereal causes of neuroretinitis [74]. Although some cases progress to meningitis, osteomyelitis, encephalitis, and endocarditis [75]. Diagnosing infections caused by *Bartonella* is

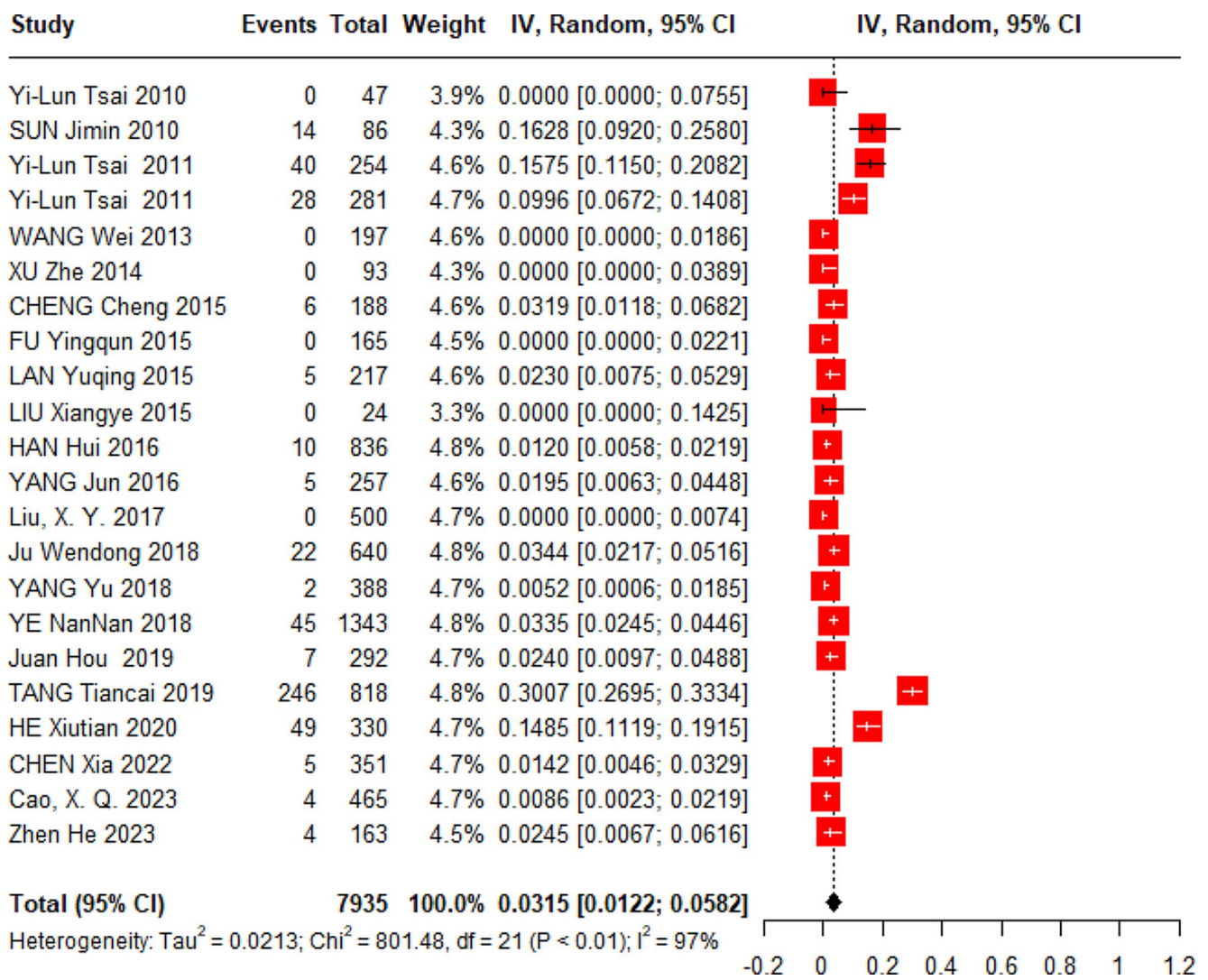


Fig. 3 Forest plot for the *Bartonella* infection rates (random effects model)

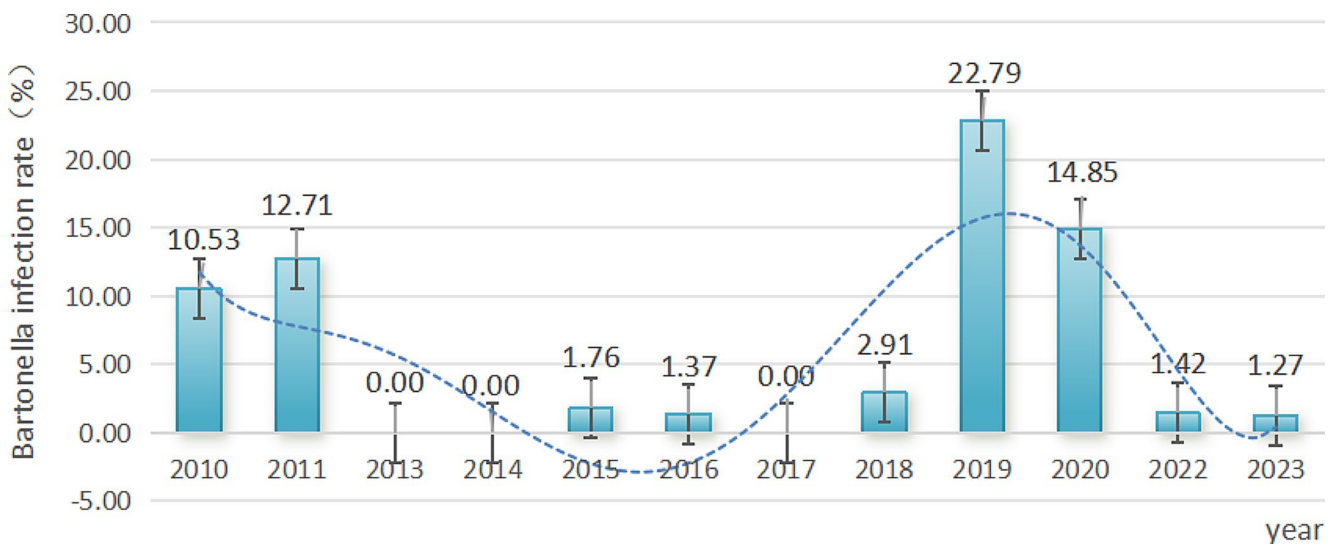


Fig. 4 *Bartonella* infection rates and trend in ticks in China according to the included studies

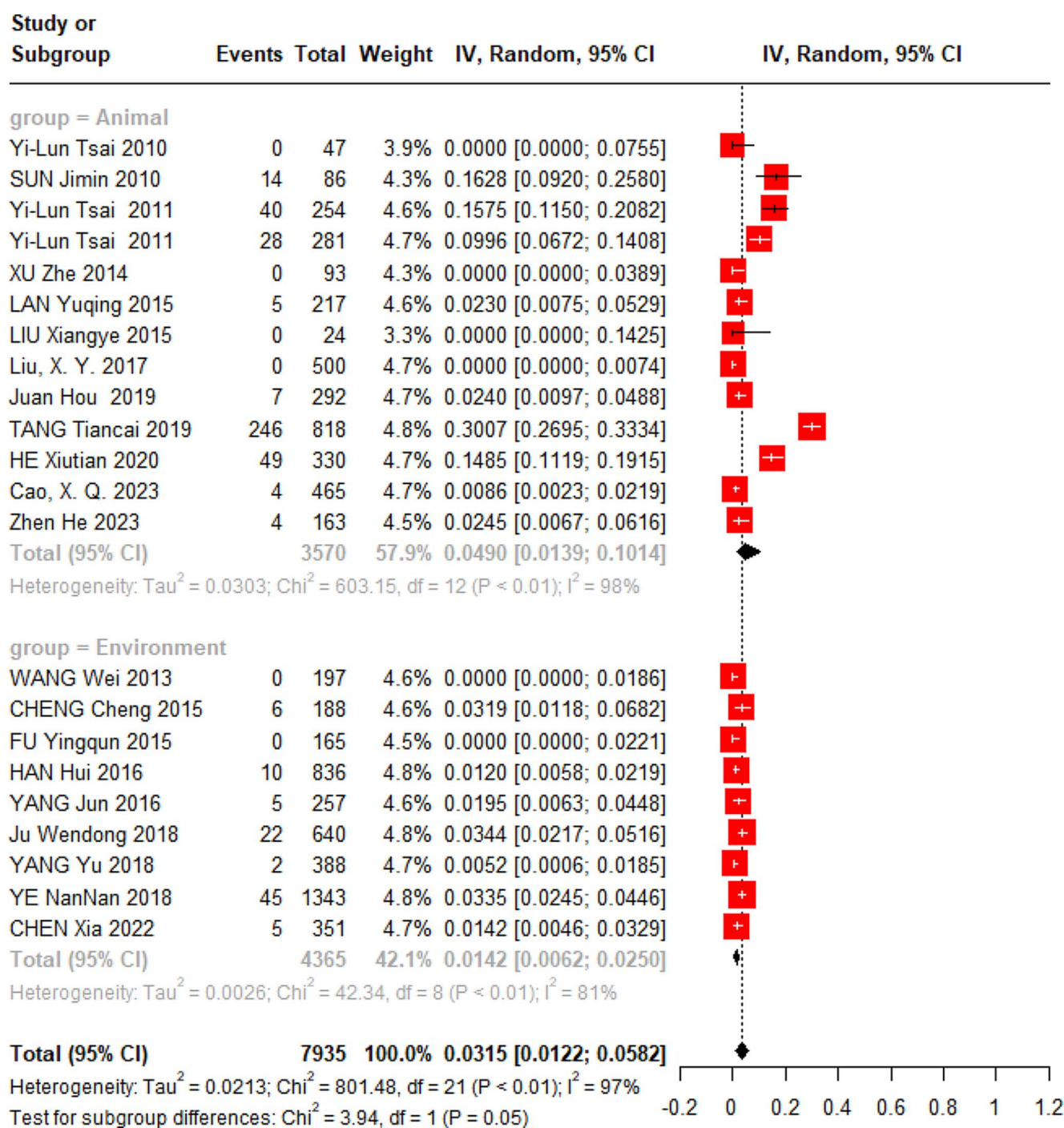


Fig. 5 Forest plot of *Bartonella* infection rate of ticks with different living habits (random effects model)

difficult due to the complex clinical symptoms and features of the pathogen [76].

The present study has four major limitations. First, the included studies encompassed a limited number of provinces, potentially introducing substantial errors in assessing the national rate of *Bartonella* infection in ticks. Second, the sample size of the ticks varied considerably across studies. The calculation of the overall

infection rate was not weighted; it simply aggregated the number of positive detections. Third, we excluded papers that lacked complete data on prevalence, which may have resulted in substantial data loss. Fourth, most studies in this paper employed PCR for pathogen detection, while Next Generation Sequencing (NGS) technology can identify a broader range of tick-associated bacteria. Prospective studies based on NGS findings can be instrumental in

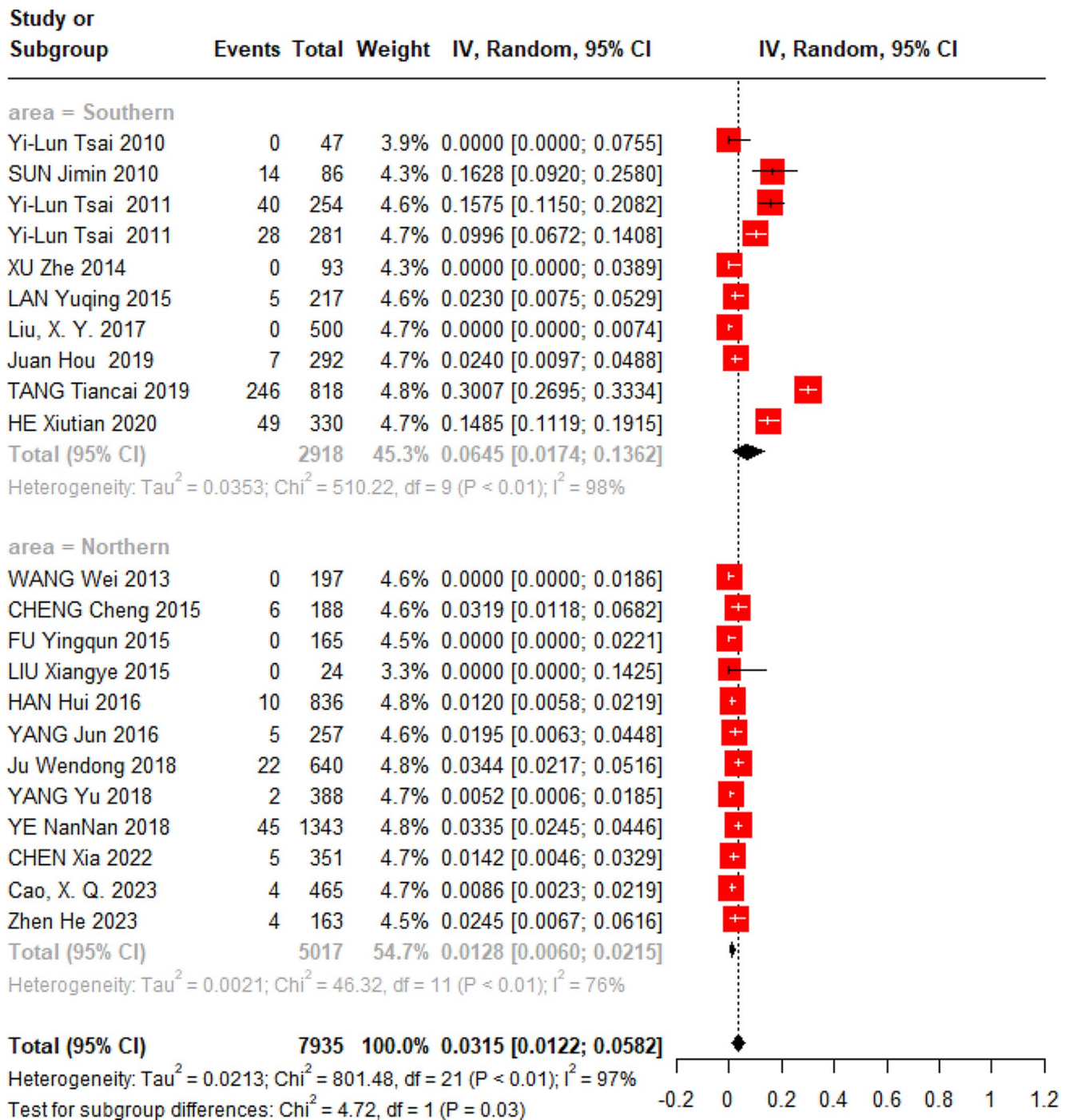


Fig. 6 Forest plot of *Bartonella* infection rates in different regions (random effects model)

preventing TBD [77]. Finally, the presence of *Bartonella* in ticks does not always mean that *Bartonella* is spread by ticks. Further studies are needed to evaluate the vector role of ticks. These findings underscore the imperative for future research on tick-associated bacteria using NGS, with a specific focus on medically relevant species to prevent TBD.

Conclusion

Ticks act as carriers for *Bartonella*, with ticks found on animals carrying more pathogens than those found in the environment, imposing a substantial disease burden. Analyzing the vector capacity of ticks is crucial in aiding public health efforts to assess the role ticks play in *Bartonella* transmission. This knowledge is indispensable for

Fig. 7 Funnel chart

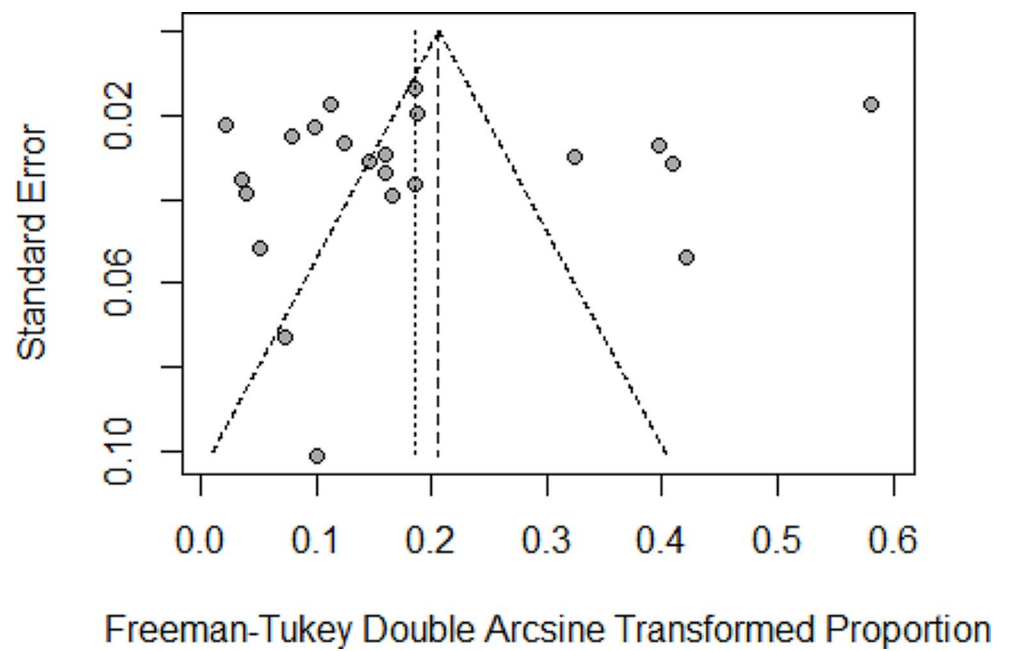
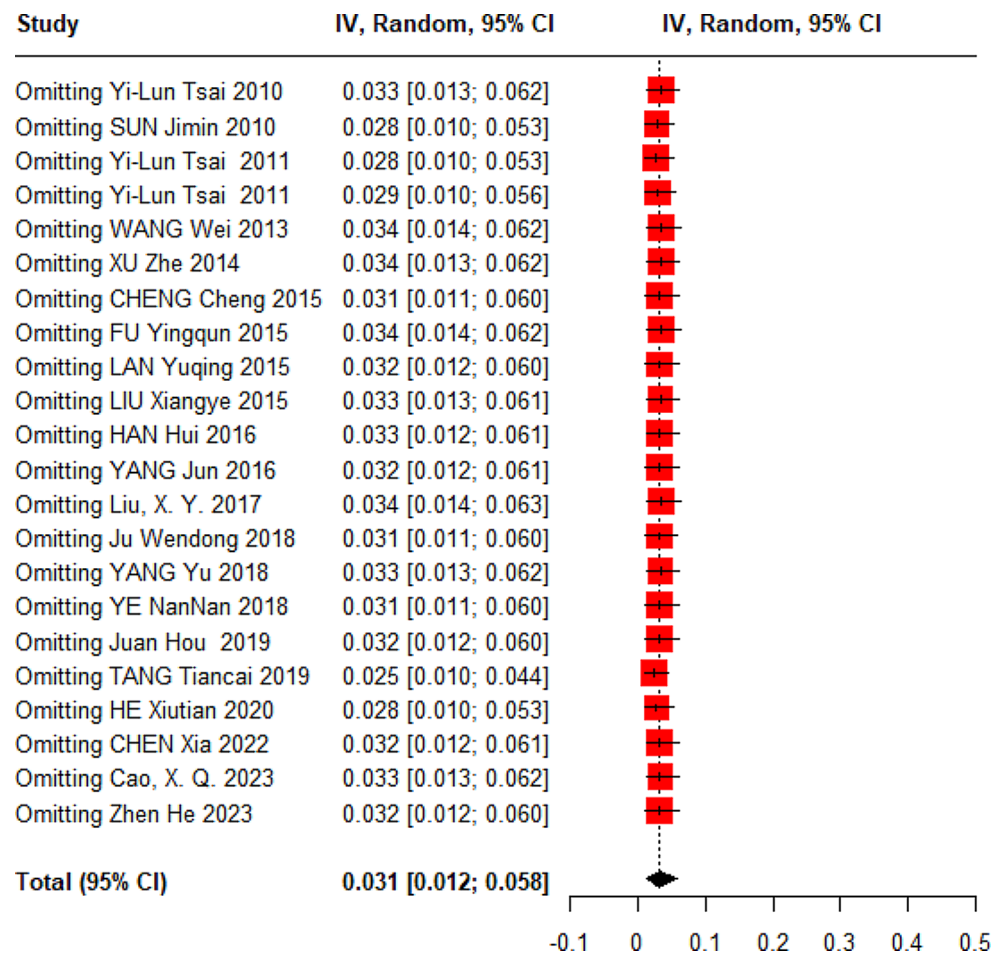


Fig. 8 Sensitivity analysis of inclusion studies



the prevention of *Bartonellosis*, particularly since there are no specific treatments currently available.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11686-024-00893-0>.

Funding This work was supported by National Natural Science Foundation of China [Grant No. 82273689]; Key Research and Development Program of Shaanxi [Grant No. 2024SF-YBXM-289].

Declarations

Competing Interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

References

- Nelson CA, Saha S, Mead PS (2016) Cat-scratch disease in the United States, 2005–2013[J]. *Emerg Infect Dis* 22(10):1741–1746. <https://doi.org/10.3201/eid2210.160115>
- Muhldorfer K (2013) Bats and bacterial pathogens: a review[J]. *Zoonoses Public Health* 60(1):93–103. <https://doi.org/10.1111/j.1863-2378.2012.01536.x>
- Boulouis HJ, Chang CC, Henn JB et al (2005) Factors associated with the rapid emergence of zoonotic *Bartonella* infections[J]. *Vet Res* 36(3):383–410. <https://doi.org/10.1051/vetres:2005009>
- Chomel BB, Boulouis HJ, Maruyama S et al (2006) *Bartonella* spp. in pets and effect on human health[J]. *Emerg Infect Dis* 12(3):389–394. <https://doi.org/10.3201/eid1203.050931>
- Klotz SA, Ianas V, Elliott SP (2011) Cat-scratch disease[J]. *Am Fam Physician* 83(2):152–155
- Ji-min S, Liang L, Qi-yong L et al (2010) Molecular epidemiological investigation of *Bartonella* infection in ticks in Zhejiang Province[J]. *Chin J Vector Biol Control* 21(03):232–234
- Spach DH, Koehler JE (1998) *Bartonella*-associated infections[J]. *Infect Dis Clin North Am* 12(1):137–155. [https://doi.org/10.1016/s0891-5520\(05\)70414-1](https://doi.org/10.1016/s0891-5520(05)70414-1)
- Krugel M, Krol N, Kempf VAJ et al (2022) Emerging rodent-associated *Bartonella*: a threat for human health?[J]. *Parasit Vectors* 15(1):113. <https://doi.org/10.1186/s13071-022-05162-5>
- Zangwill KM, Hamilton DH, Perkins BA et al (1993) Cat scratch disease in connecticut. Epidemiology, risk factors, and evaluation of a new diagnostic test[J]. *N Engl J Med* 329(1):8–13. <https://doi.org/10.1056/NEJM199307013290102>
- Lucey D, Dolan MJ, Moss CW et al (1992) Relapsing illness due to *Rochalimaea henselae* in immunocompetent hosts: implication for therapy and new epidemiological associations[J]. *Clin Infect Dis* 14(3):683–688. <https://doi.org/10.1093/clinids/14.3.683>
- Bowman AS, Nuttall PA (2008) *Ticks: biology, disease and control*. Cambridge University Press
- Parola P (2004) Tick-borne rickettsial diseases: emerging risks in Europe[J]. *Comp Immunol Microbiol Infect Dis* 27(5):297–304. <https://doi.org/10.1016/j.cimid.2004.03.006>
- Graves SR, Stenos J (2017) Tick-borne infectious diseases in Australia[J]. *Med J Aust* 206(7):320–324. <https://doi.org/10.5694/mja17.00090>
- Dehghani M, Kazemi Shariat Panahi H, Holmes EC et al (2019) Human tick-borne diseases in Australia[J]. *Front Cell Infect Microbiol* 9:3. <https://doi.org/10.3389/fcimb.2019.00003>
- Parola P, Paddock CD, Socolovschi C et al (2013) Update on tick-borne rickettsioses around the world: a geographic approach[J]. *Clin Microbiol Rev* 26(4):657–702. <https://doi.org/10.1128/CMR.00032-13>
- Chang CC, Chomel BB, Kasten RW et al (2001) Molecular evidence of *Bartonella* spp. in questing adult *Ixodes pacificus* ticks in California[J]. *J Clin Microbiol* 39(4):1221–1226. <https://doi.org/10.1128/JCM.39.4.1221-1226.2001>
- de la Fuente J, Estrada-Pena A, Venzal JM et al (2008) Overview: ticks as vectors of pathogens that cause disease in humans and animals[J]. *Front Biosci* 13:6938–6946. <https://doi.org/10.2741/3200>
- Hempleman SC, Warburton SJ (2013) Comparative embryology of the carotid body[J]. *Respir Physiol Neurobiol* 185(1):3–8. <https://doi.org/10.1016/j.resp.2012.08.004>
- Kong Y, Zhang G, Jiang L et al (2022) Metatranscriptomics reveals the diversity of the tick virome in Northwest China[J]. *Microbiol Spectr* 10(5):e0111522. <https://doi.org/10.1128/spectrum.01115-22>
- Sonenshine DE (2018) Range expansion of tick disease vectors in North America: implications for spread of tick-borne disease[J]. *Int J Environ Res Public Health* 15(3). <https://doi.org/10.3390/ijerph15030478>
- Madison-Antenucci S, Kramer LD, Gebhardt LL et al (2020) Emerging tick-borne diseases[J]. *Clin Microbiol Rev* 33(2). <https://doi.org/10.1128/CMR.00083-18>
- Fang LQ, Liu K, Li XL et al (2015) Emerging tick-borne infections in mainland China: an increasing public health threat[J]. *Lancet Infect Dis* 15(12):1467–1479. [https://doi.org/10.1016/S1473-3099\(15\)00177-2](https://doi.org/10.1016/S1473-3099(15)00177-2)
- Zhao GP, Wang YX, Fan ZW et al (2021) Mapping ticks and tick-borne pathogens in China[J]. *Nat Commun* 12(1):1075. <https://doi.org/10.1038/s41467-021-21375-1>
- Tsai YL, Chuang ST, Chang CC et al (2010) *Bartonella* species in small mammals and their ectoparasites in Taiwan[J]. *Am J Trop Med Hyg* 83(4):917–923. <https://doi.org/10.4269/ajtmh.2010.10-0083>
- Tsai YL, Chomel BB, Chang CC et al (2011) *Bartonella* and *Babesia* infections in cattle and their ticks in Taiwan[J]. *Comp Immunol Microbiol Infect Dis* 34(2):179–187. <https://doi.org/10.1016/j.cimid.2010.11.003>
- Tsai YL, Lin CC, Chomel BB et al (2011) *Bartonella* infection in shelter cats and dogs and their ectoparasites[J]. *Vector Borne Zoonotic Dis* 11(8):1023–1030. <https://doi.org/10.1089/vbz.2010.0085>
- Wang W, Li I (2013) Investigation on ticks and the pathogens they could carry in Tianjin[J]. *Chin J Hyg Insect & Equip* 19(03):220–222. <https://doi.org/10.19821/j.1671-2781.2013.03.016>
- Zhe X, Xuhon X, Yilong Z et al (2014) Comprehensive surveillance of tick-borne diseases in Jiande, Zhejiang Province China[J]. *Chin J Vector Biol & Control* 25(4)
- Cheng C, Wen-dong J, dan J, et al (2015) Investigation of emerging tick-borne diseases at Heilongjiang ports[J]. *Chinese Frontier*

- Health Quarantine.;38(03):176–181. <https://doi.org/10.16408/j.1004-9770.2015.03.007>
30. Ying-qun F, Ting-ting L, Yong H et al (2015) Investigation of ticks and carried pathogens on Heixiazhi island[J]. Chin Frontier Health Quarantine 38(02):119–123. <https://doi.org/10.16408/j.1004-9770.2015.02.011>
 31. Yu-qing L, Feng L, Jin-bo H et al (2015) Surveillance of tick-borne infections during 2012–2013 in Lishui, Zhejiang[J]. Chin J Vector Biol Control 26(5):512–515. <https://doi.org/10.11853/j.issn.1003.4692.2015.05.022>
 32. Liu X, Zheng C, Li X et al (2015) Research on the pathogenic infection of *Haemaphysalis longicornis* ticks parasitizing goats in Yiyuan County, Shandong Province[J]. Acta Academiae Medicinae Xuzhou 35(12):837–840
 33. Han H, Yang Y, Zhao X et al (2016) Monitoring for tick and tick-borne pathogens at Inner Mongolia Ports[J]. Acta Parasitol Med Entomol Sin.;23(4)
 34. Jun Y, Yanmei W, Wendong J et al (2016) Investigation on emerging tick-borne pathogens and co-infection in ticks in lava area of Xunke County, Heilongjiang Province[J]. Chin J Vector Biol Control 27(04):341–344
 35. Liu XY, Gong XY, Zheng C et al (2017) Molecular epidemiological survey of bacterial and parasitic pathogens in hard ticks from eastern China[J]. Acta Trop 167:26–30. <https://doi.org/10.1016/j.actatropica.2016.12.010>
 36. Ju W, Wang Y, Xu N et al (2018) Investigation on Bartonella infection in rodents and ticks at Heihe Airport in Heilongjiang Province[J]. Port Health Control 23(02):60–63. <https://doi.org/10.16408/j.1004-9770.2015.03.007>
 37. Yu Y, Yan-fei G, Yang C et al (2018) Investigation on tick-borne pathogens in Inner Mongolia Manchuria port area during 2012–2014[J]. Chin J Vector Biol Control 29(02):147–150
 38. Ye N, Pei X, Sun S (2018) Investigation of the ticks in border trade regions of Heihe[J]. Chin J Zoonoses 34(08):761–767. <https://doi.org/10.3969/j.issn.1002-2694.2018.00.128>
 39. Hou J, Ling F, Liu Y et al (2019) A molecular survey of Anaplasma, Ehrlichia, Bartonella, and Theileria in ticks collected from southeastern China[J]. Exp Appl Acarol 79(1):125–135. <https://doi.org/10.1007/s10493-019-00411-2>
 40. Tiancai T, chengcheng L, Dongbo Y et al (2019) Molecular detection of Bartonella infection in ixodid ticks collected from yaks in Shiqu County of Sichuan Province[J]. Acta Agriculturae Zhejiangensis 31(07):1066–1072. <https://doi.org/10.3969/j.issn.1004-1524.2019.07.05>
 41. Xiutian H, Yang X, Dongbo Y et al (2020) PCR detection and phylogenetic analysis of Bartonella spp. and Anaplasma spp. in Ixodid ticks collected from Yak and Plateau Pika in Songpan County of Sichuan Province[J]. Acta Vet Et Zootechnica Sinica 51(06):1438–1446. <https://doi.org/10.11843/j.issn.0366-6964.2020.06.027>
 42. Xia C, Lei N, Hui-jie L et al (2022) Surveillance of ticks and tick-borne pathogens at Fuyuan port in Heilongjiang Province from 2019 to 2021[J]. Chin Frontier Health Quarantine 45(5):357–360. <https://doi.org/10.16408/j.1004-9770.2022.05.005>
 43. Cao XQ, Gu XL, Zhang L et al (2023) Molecular detection of Rickettsia, Anaplasma, and Bartonella in ticks from free-ranging sheep in Gansu Province, China[J]. Ticks Tick Borne Dis 14(3):102137. <https://doi.org/10.1016/j.ttbdis.2023.102137>
 44. He Z, Fu T, Yan M et al (2023) Analysis of epidemiological characteristics of pathogens carried by ticks in Qinling Area[J]. Adv Clin Med 13(11). <https://doi.org/10.12677/acm.2023.13112375>
 45. Boulanger N, Boyer P, Talagrand-Reboul E et al (2019) Ticks and tick-borne diseases[J]. Med Mal Infect 49(2):87–97. <https://doi.org/10.1016/j.medmal.2019.01.007>
 46. Diaz-Sanchez AA, Obregon D, Santos HA et al (2023) Advances in the epidemiological surveillance of tick-borne pathogens[J]. Pathogens 12(5). <https://doi.org/10.3390/pathogens12050633>
 47. Edvinsson M, Norlander C, Nilsson K et al (2021) Bartonella spp. seroprevalence in tick-exposed Swedish patients with persistent symptoms[J]. Parasit Vectors 14(1):530. <https://doi.org/10.1186/s13071-021-05043-3>
 48. Cutler SJ, Vayssier-Taussat M, Estrada-Pena A et al (2021) Tick-borne diseases and co-infection: current considerations[J]. Ticks Tick Borne Dis 12(1):101607. <https://doi.org/10.1016/j.ttbdis.2020.101607>
 49. Bacon EA, Kopsco H, Gronemeyer P et al (2022) Effects of climate on the variation in abundance of three tick species in Illinois[J]. J Med Entomol 59(2):700–709. <https://doi.org/10.1093/jme/tjab189>
 50. Estrada-Pena A (2023) The climate niche of the invasive tick species *Hyalomma marginatum* and *Hyalomma rufipes* (Ixodidae) with recommendations for modeling exercises[J]. Exp Appl Acarol 89(2):231–250. <https://doi.org/10.1007/s10493-023-00778-3>
 51. Estrada-Pena A (2009) Tick-borne pathogens, transmission rates and climate change[J]. Front Biosci (Landmark Ed) 14(7):2674–2687. <https://doi.org/10.2741/3405>
 52. Sands BO, Bryer KE, Wall R (2021) Climate and the seasonal abundance of the tick *Dermacentor reticulatus*[J]. Med Vet Entomol 35(3):434–441. <https://doi.org/10.1111/mve.12518>
 53. Barker SC, Walker AR (2014) Ticks of Australia. The species that infest domestic animals and humans[J]. Zootaxa 3816:1–144. <https://doi.org/10.11646/zootaxa.3816.1.1>
 54. Bakirci S, Aysul N, Bilgic HB et al (2019) Tick bites on humans in southwestern region of Turkey: species diversity[J]. Turkiye Parazit Derg 43(1):30–35. <https://doi.org/10.4274/tpd.galenos.2019.6219>
 55. Ogden NH, Ben Beard C, Ginsberg HS et al (2021) Possible effects of climate change on Ixodid ticks and the pathogens they transmit: predictions and observations[J]. J Med Entomol 58(4):1536–1545. <https://doi.org/10.1093/jme/tjaa220>
 56. Zhang YK, Zhang XY, Liu JZ (2019) Ticks (Acari: Ixodoidea) in China: geographical distribution, host diversity, and specificity[J]. Arch Insect Biochem Physiol 102(3):e21544. <https://doi.org/10.1002/arch.21544>
 57. Nasirian H (2022) Ticks infected with Crimean-Congo hemorrhagic fever virus (CCHFV): a decision approach systematic review and meta-analysis regarding their role as vectors[J]. Travel Med Infect Dis 47:102309. <https://doi.org/10.1016/j.tmaid.2022.102309>
 58. Randolph SE (2011) Transmission of tick-borne pathogens between co-feeding ticks: Milan Labuda's enduring paradigm[J]. Ticks Tick Borne Dis 2(4):179–182. <https://doi.org/10.1016/j.ttbdis.2011.07.004>
 59. Moraes-Filho J, Costa FB, Gerardi M et al (2018) Rickettsia rickettsii Co-feeding transmission among *Amblyomma aureolatum* ticks[J]. Emerg Infect Dis 24(11):2041–2048. <https://doi.org/10.3201/eid2411.180451>
 60. Sun J, Liu Q, Lu L et al (2008) Coinfection with four genera of bacteria (*Borrelia*, *Bartonella*, *Anaplasma*, and *Ehrlichia*) in *Haemaphysalis longicornis* and *Ixodes sinensis* ticks from China[J]. Vector Borne Zoonotic Dis 8(6):791–795. <https://doi.org/10.1089/vbz.2008.0005>
 61. Zhao C, Zhang X, Si X et al (2022) Hedgehogs as amplifying hosts of severe fever with thrombocytopenia syndrome virus, China[J]. Emerg Infect Dis 28(12):2491–2499. <https://doi.org/10.3201/eid2812.220668>
 62. Qiu H, Lv Q, Chang Q et al (2022) Microbiota community structure and interaction networks within *Dermacentor silvarum*, *Ixodes persulcatus*, and *Haemaphysalis concinna*[J]. Anim (Basel) 12(23). <https://doi.org/10.3390/ani12233237>

63. Van Treuren W, Ponnusamy L, Brinkerhoff RJ et al (2015) Variation in the microbiota of Ixodes ticks with regard to geography, species, and sex[J]. *Appl Environ Microbiol* 81(18):6200–6209. <https://doi.org/10.1128/AEM.01562-15>
64. Sperling JL, Silva-Brandao KL, Brandao MM et al (2017) Comparison of bacterial 16S rRNA variable regions for microbiome surveys of ticks[J]. *Ticks Tick Borne Dis* 8(4):453–461. <https://doi.org/10.1016/j.ttbdis.2017.02.002>
65. Li T, Liu M, Zhang TT et al (2018) The life cycle and development characteristics of *Dermacentor everestianus* (Acari: Ixodidae) under field conditions in Qinghai-Tibet Plateau[J]. *Exp Appl Acarol* 76(4):513–522. <https://doi.org/10.1007/s10493-018-0325-0>
66. Weinert LA, Werren JH, Aebi A et al (2009) Evolution and diversity of *Rickettsia* bacteria[J]. *BMC Biol* 7:6. <https://doi.org/10.1186/1741-7007-7-6>
67. Rochlin I, Toledo A (2020) Emerging tick-borne pathogens of public health importance: a mini-review[J]. *J Med Microbiol* 69(6):781–791. <https://doi.org/10.1099/jmm.0.001206>
68. Seo JW, Kim D, Yun N et al (2021) Clinical update of severe fever with thrombocytopenia syndrome[J]. *Viruses* 13(7). <https://doi.org/10.3390/v13071213>
69. Guo WB, Shi WQ, Wang Q et al (2021) Distribution of *Dermacentor silvarum* and associated pathogens: meta-analysis of global published data and a field survey in China[J]. *Int J Environ Res Public Health* 18(9). <https://doi.org/10.3390/ijerph18094430>
70. Rubel F, Brugger K, Belova OA et al (2020) Vectors of disease at the northern distribution limit of the genus *Dermacentor* in Eurasia: *D. reticulatus* and *D. silvarum*[J]. *Exp Appl Acarol* 82(1):95–123. <https://doi.org/10.1007/s10493-020-00533-y>
71. Hojgaard A, Osikowicz LM, Rizzo MF et al (2022) Using next generation sequencing for molecular detection and differentiation of *Anaplasma phagocytophilum* variants from host seeking *Ixodes scapularis* ticks in the United States[J]. *Ticks Tick Borne Dis* 13(6):102041. <https://doi.org/10.1016/j.ttbdis.2022.102041>
72. Deng H, Pang Q, Zhao B et al (2018) Molecular mechanisms of *Bartonella* and mammalian erythrocyte interactions: a review[J]. *Front Cell Infect Microbiol* 8:431. <https://doi.org/10.3389/fcimb.2018.00431>
73. Zangwill KM (2013) Cat scratch disease and other *Bartonella* infections[J]. *Adv Exp Med Biol* 764:159–166. https://doi.org/10.1007/978-1-4614-4726-9_13
74. Yap SM, Saeed M, Logan P et al (2020) *Bartonella* neuroretinitis (cat-scratch disease)[J]. *Pract Neurol* 20(6):505–506. <https://doi.org/10.1136/practneurol-2020-002586>
75. Florin TA, Zaoutis TE, Zaoutis LB (2008) Beyond cat scratch disease: widening spectrum of *Bartonella henselae* infection[J]. *Pediatrics* 121(5):e1413–1425. <https://doi.org/10.1542/peds.2007-1897>
76. Iannino F, Salucci S, Di Provvio A et al (2018) *Bartonella* infections in humans dogs and cats[J]. *Vet Ital* 54(1):63–72. <https://doi.org/10.12834/VetIt.398.1883.2>
77. Che Lah EF, Ahamad M, Dmitry A et al (2023) Metagenomic profile of the bacterial communities associated with *Ixodes granulatus* (Acari: Ixodidae): a potential vector of tick-borne diseases[J]. *J Med Entomol* 60(4):753–768. <https://doi.org/10.1093/jme/tjad044>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.