



Geographical distribution of *Ixodes persulcatus* and associated pathogens: Analysis of integrated data from a China field survey and global published data

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ABSTRACT

The increasing incidence and range expansion of tick-borne diseases have caused global threats to human and animal health under the background of climate and socioeconomic changes. As an efficient vector in transmission of tick-borne diseases, a growing burden caused by *Ixodes persulcatus* and associated pathogens could not be underestimated. This study summarized the distribution, hosts, and pathogens of *I. persulcatus*, and predicted the suitable habitats of this tick species worldwide. An integrated database involving a field survey, reference book, literature review, and related website was constructed. Location records of *I. persulcatus* and associated pathogens were incorporated into distribution maps using ArcGIS software. Positive rates for *I. persulcatus*-associated agents were estimated by meta-analysis. The global distribution of the tick species was predicted using Maxent model. *I. persulcatus* was distributed in 14 countries across the Eurasian continent, involving Russia, China, Japan, and several Baltic Sea states, which ranged between 21°N to 66°N. The tick species fed on 46 species of hosts, and 51 tick-borne agents could be harbored by *I. persulcatus*. The predictive model showed that *I. persulcatus* could be predominantly distributed in northern Europe, western Russia, and northern China. Our study fully clarified the potential public health risks posed by *I. persulcatus* and *I. persulcatus*-borne pathogens. Surveillance and control measures of tick-borne diseases should be enhanced to promote the health of humans, animals, and ecosystems.

1. Introduction

Partly due to the climate and socioeconomic changes, tick populations are increasing and their geographic ranges are expanding globally, which provides suitable habitats for ticks and their harbored pathogens [1]. The last several decades have witnessed a steady and continued rise in the number of recognized tick-borne pathogens and the number of tick-borne disease cases, posing a serious and growing public health threat [2–4]. In the United States, the reported tick-borne disease

cases nearly tripled from 2004 to 2017 [4]. *I. persulcatus*, one of the most crucial vectors of human and animal diseases in the northern hemisphere, is distributed throughout Eurasia [5]. It readily feeds on humans and has been implicated as the vector of various microbial pathogens, such as tick-borne encephalitis virus (TBEV), *Anaplasma phagocytophilum*, *Babesia divergens*, and *Borrelia afzelii*, causing multi-organ and multi-system damage [5–7]. The Alongshan virus, a newly discovered tick-borne virus in 2019, was also closely associated with the tick species [8].

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Although there have been studies on several pathogens carried by *I. persulcatus*, most previous studies are limited to a certain area or laboratory characteristics of pathogens, related epidemiological data is insufficient. And there is a lack of effective nationally tick surveillance in many countries to identify the range expansion of the tick. The global health threat posed by *I. persulcatus* and *I. persulcatus*-borne diseases remains obscure. In this study, we built a dataset of *I. persulcatus* from multiple data sources, conducted an extensive investigation of the geographical distribution, hosts, and associated pathogens of *I. persulcatus*, predicted the suitable areas for the tick species on a global scale, and provided targeted guidance for the prevention and control of *I. persulcatus*-borne diseases.

2. Methods

2.1. Data collection and extraction

Multiple data sources of *I. persulcatus* involving a field survey, literature review, reference book, and related website were integrated into a comprehensive dataset. Our group conducted a field survey in 31 provinces, autonomous regions, and municipalities of mainland China. All tick samples collected from vegetation and animals were identified to species by an entomologist based on morphological features. Ticks identified as *I. persulcatus* were included in the present study, and all collected locations of *I. persulcatus* were listed in Supplementary Table 1. We also extracted the distribution data of *I. persulcatus* from the reference book, *Fauna Sinica-Arachnida Ixodida*, the website of the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>), and published literatures.

2.2. Literature review

2.2.1. Review protocol

Literature searches were conducted by two independent reviewers. We searched PubMed, China National Knowledge Infrastructure (CNKI), and WanFang Database for articles between January 1, 1954, and September 30, 2021 by using the search terms “*Ixodes persulcatus*” and the Chinese name for *Ixodes persulcatus* (detailed procedures for literature search are provided in Supplementary Figure 1 and Supplementary Data 1). Articles with search terms included in any part of their content were retrieved.

2.2.2. Eligible criteria selection

Two independent reviewers assessed the eligibility of each article after duplicates removal. Published full articles were eligible for inclusion if they met the following criteria: (1) studies with sufficient detail on collection locations of *I. persulcatus* (at county or prefecture level); (2) language restrictions in English or Chinese. All irrelevant or review articles were excluded.

2.2.3. Estimation of pathogen prevalence

A meta-analysis was conducted to estimate the combined positive rate and 95% confidence interval (CI) of each *I. persulcatus*-associated pathogen. Articles that reported the exact number of tested *I. persulcatus* were included. The positive rate was calculated by the number of positive ticks divided by total ticks and without a 95% CI, when there was only one study identifying a certain species of pathogen. The combined positive rate and 95% CI were estimated using R software (version 4.0.5, meta package), when the number of included studies was two or more. We quantified the heterogeneity of the data by I^2 statistic. I^2 above 50% indicated that the heterogeneity was significant and the random effects model was applied. Otherwise, the fixed effects model was used.

2.3. Environmental variables

Nineteen bioclimatic variables, including annual mean temperature,

mean diurnal range, isothermality, temperature seasonality, max temperature of warmest month, min temperature of coldest month, annual range of temperature, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarters and precipitation of coldest quarter, and elevation data were downloaded from WorldClim (www.worldclim.org). Variables of slope and aspect were obtained using the Spatial Analyst Tool. Vegetation (Percent Tree Cover) and land cover (GLCNMO) were available from the Resource and Environmental Science and Data Center of Global Map (<https://globalmaps.github.io/>). All these 24 environmental variables with a spatial resolution of 5 arc-min (~10 km) were used to establish the prediction model for the global potential distribution of *I. persulcatus* (see Supplementary Table 2 for details).

2.4. Distribution of *I. persulcatus* and associated pathogens

Geographical distribution of *I. persulcatus* and its associated pathogens were plotted by ArcGIS 10.2 software. The latitude and longitude coordinates of collected locations of *I. persulcatus* were applied for mapping, and the administrative region centroids were used when the exact locations were not available.

2.5. Prediction model of distribution of *I. persulcatus*

An ecological niche model (ENM) was applied for predicting the distribution of *I. persulcatus* [9,10]. Locations indicated by administrative region centroids were not taken into account in our model. A total of 349 geographic records were finally retained (Supplementary Table 3). R software (kuenm package) was used to determine the model parameters. The ENM model was performed in Maxent software (version 3.4.1) (the detailed procedures of model building are provided in Supplementary Data 2).

3. Results

3.1. Geographical distribution of *I. persulcatus*

As shown in Supplementary Fig. 1, 11,626 articles were identified from literature search, and 374 articles that met our inclusion and exclusion criteria were finally included for further analysis (see Supplementary Data 1 for details). A total of 2179 records of distribution of *I. persulcatus* were collected, of which 1209 were from literature review, 27 were from field survey, 52 were from the reference book and 891 were from GBIF. After removing duplicates, 967 records were included in the integrated database.

I. persulcatus was only found distributed between 21°–66° latitude in the northern hemisphere, involving 14 countries across the Eurasian continent, including Russia, China, Japan, Estonia, Finland, Kazakhstan, Latvia, South Korea, Sweden, Mongolia, Lithuania, Kyrgyzstan, Ukraine, and Poland (Figs. 1 and 2A, Supplementary Fig. 2). Russia had the most distribution records of *I. persulcatus*. The tick species was present in 31 regions throughout Russia, such as Altai, Novosibirsk, and Omsk oblast, and was most abundant in the southwestern areas. In China, the tick species was most prevalent in the northeast and northwest areas, including Heilongjiang, Jilin, Liaoning, Inner Mongolia, and Xinjiang (Fig. 2B). In Japan, *I. persulcatus* was mainly distributed in the central areas and Hokkaido. In addition, *I. persulcatus* was identified in the northern and eastern Europe, especially the countries that have shorelines along the Baltic Sea, involving Sweden, Finland, Estonia, Latvia, Lithuania, and Poland (Fig. 2A).

3.2. Hosts of *I. persulcatus*

As shown in Fig. 3, *I. persulcatus* was reported to feed on 46 species of hosts, which belong to 22 families. *Canis lupus* (dog) was known as common animal host of *I. persulcatus*, and had been parasitized by the tick species in 5 countries. A total of 18 bird species belonging to 10 families were recorded as hosts of *I. persulcatus*, with only one species (*Turdus pallidus*) found in Japan and the others in Russia. *I. persulcatus* had the most diverse range of host animals in Russia, involving 31 species, of which 21 were only found in this country. *I. persulcatus* had been collected from 17 species of animals in China, and 9 species were distinctive from other countries. In Japan, the hosts of *I. persulcatus* included 7 species of animals, most of which were medium-sized mammals. A broad range of other animals can be parasitized by the tick species, which were identified in Sweden, South Korea, Finland, Estonia, and Latvia.

3.3. Positive rate and distribution of *I. persulcatus*-associated pathogens

As shown in Fig. 4, 51 species of microorganisms, including 33 human pathogens, 6 animal pathogens, and 12 agents with unknown risks of pathogenicity were identified in *I. persulcatus*. Nine species

belonging to the Anaplasmataceae family were detected in *I. persulcatus*. Among them, *Anaplasma* sp. *Mongolia* (27.78%), *Ehrlichia chaffeensis* (5.68%, 95%CI 1.68–11.56), and *A. phagocytophilum* (4.77%, 95%CI 3.73–5.91) had high positive rates. Eleven species of *Babesia* harbored by *I. persulcatus* were reported, with *Babesia venatorum* having the highest pooled positive rate at 0.93% (95%CI 0.50–1.48). Seven genospecies in the complex *Borrelia burgdorferi* sensu lato were found to be carried by *I. persulcatus*, among which the pooled positive rates of *Borrelia garinii* (12.80%, 95% CI 8.32–19.17) and *B. afzelii* (8.13%, 95% CI 5.09–11.76) were both high. Nine species of spotted fever group rickettsiae (SFGR) were found in *I. persulcatus*. *Candidatus Rickettsia tarasevichiae* (CRT) (26.88%, 95%CI 17.77–37.08) and *Rickettsia japonica* (21.68%) showed high pooled positive rates. Eight species of viruses were detected in *I. persulcatus*, including Alongshan virus and TBEV. Other pathogens, like *Francisella tularensis*, *Coxiella burnetii*, and *Theileria* were also detected (Supplementary Fig. 3).

Geographical distribution of human pathogens harbored by *I. persulcatus* was basically consistent with the tick species, involving 10 countries across Eurasia (Fig. 5). Pathogens were more abundant and widely distributed in Asian countries than in Europe. TBEV was the most widely distributed pathogen, involving 27 regions in 6 countries. In China, the largest variety of human pathogens (28 species) were

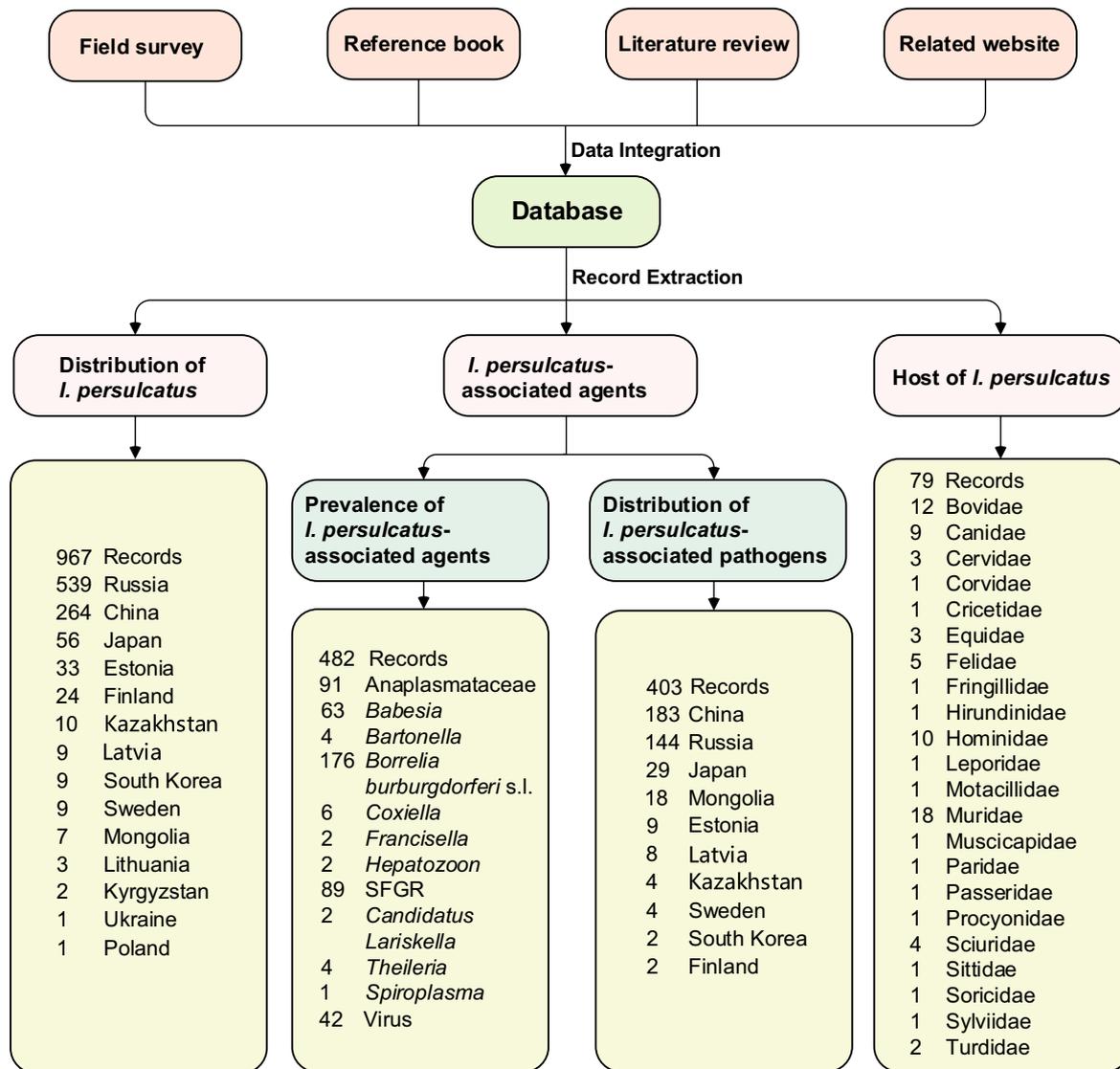


Fig. 1. Research design and records. SFGR = Spotted fever group rickettsiae.

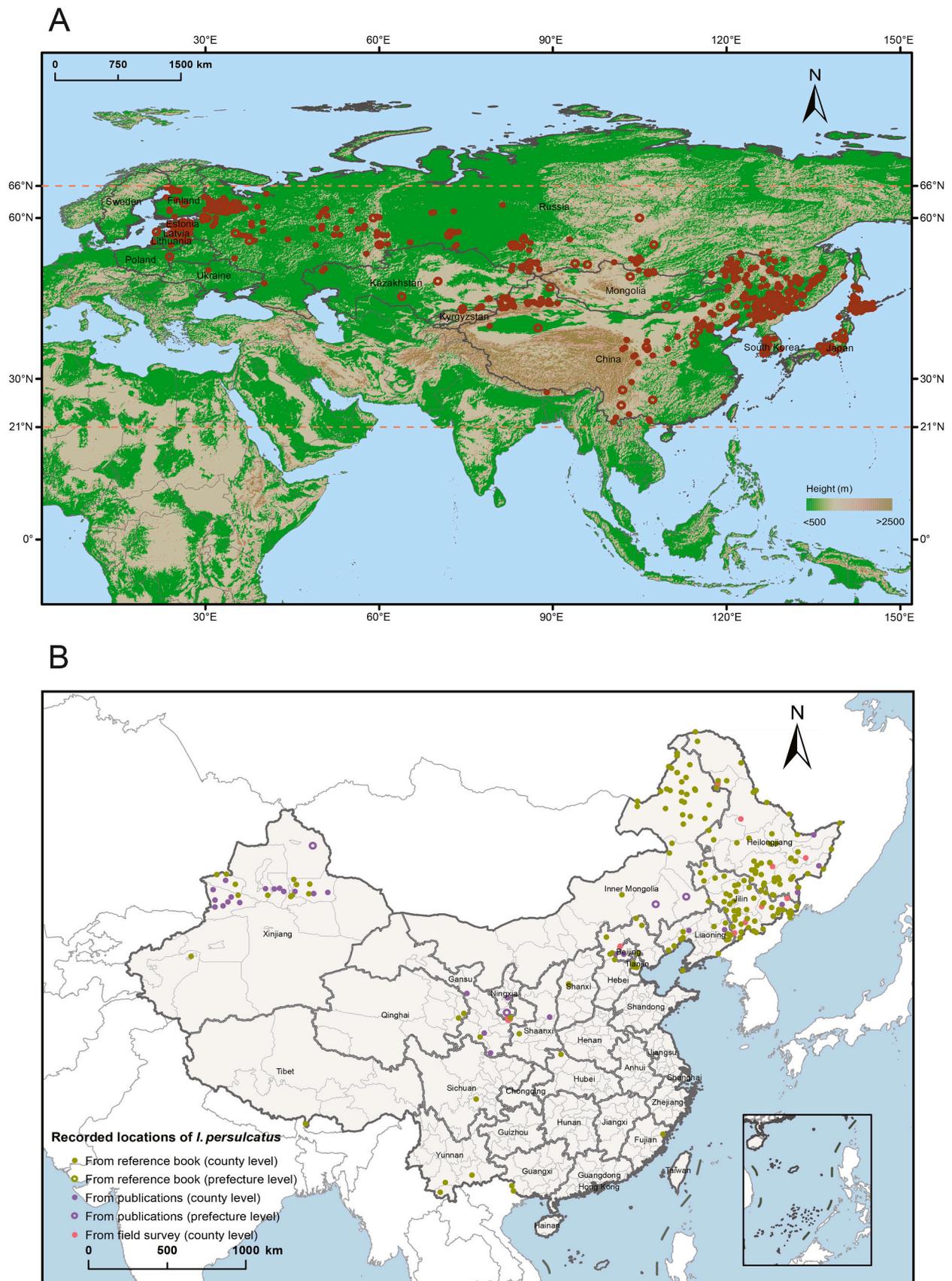


Fig. 2. Geographical distribution of *I. persulcatus*. (A) Recorded locations of *I. persulcatus* worldwide. Empty circles represent the prefecture-level regions (the first-level administrative regions of the country), and filled circles represent the county-level regions (the second-level administrative regions of the country). The tick species was distributed in the regions between 21°–66° latitude in the northern hemisphere. (B) Recorded locations of *I. persulcatus* in China.

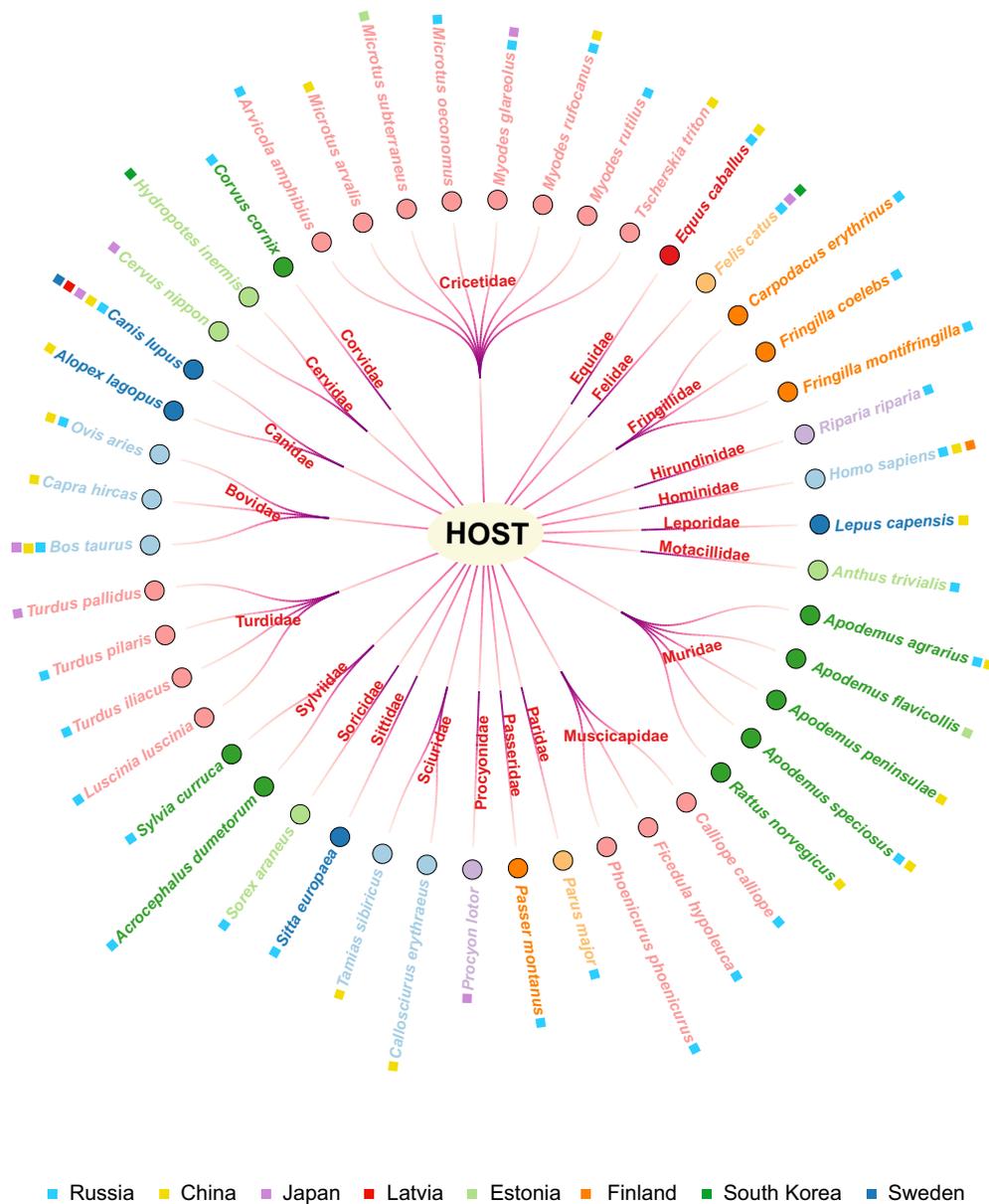


Fig. 3. Hosts of *I. persulcatus* in different countries. Names displayed in the inner circle represent the families of host, and names displayed in the outer circle represent the species of hosts. Solid squares represent countries that the hosts of *I. persulcatus* were identified. *I. persulcatus* feeds on a total of 46 species of hosts in different countries.

detected in *I. persulcatus*, including five species in the family Anaplasmataceae, four *Babesia* species, four genospecies in the complex *Borrelia burgdorferi* sensu lato, six SFGR species, seven species of viruses, *Francisella tularensis* and *Coxiella burnetii*. It is noteworthy that eight species of pathogens were only found in Northeast China, which is a densely populated area. Eighteen species of *I. persulcatus*-associated human pathogens were detected in Russia. Among them, *A. phagocytophilum* and Kemerovo virus were identified throughout the country, while *Borrelia miyamotoi* and CRT were sporadically distributed in some areas. A variety of *Borrelia burgdorferi* sensu lato and *Babesia* species were carried by *I. persulcatus* in Japan. In the Baltic Sea states, pathogens were primarily identified in Estonia and Latvia, and *Babesia* and *Borrelia burgdorferi* sensu lato were more common. In addition, there were no records of *I. persulcatus*-borne pathogens in Poland, Ukraine, Lithuania, and Kyrgyzstan.

3.4. Predicted distribution of *I. persulcatus*

In the present study, nine independent variables with the optimization parameters (feature combination = LPTH and regularization multiplier = 1.8) were finally used to develop the prediction model, including BIO18, BIO11, BIO4, BIO19, vegetation, election, BIO16, BIO2, and BIO15. The average AUC value of Maxent model with 25 replicates was 0.964 ± 0.015 , indicating the prediction effect was good. Based on the percentage contribution rate and jackknife test, precipitation of the warmest quarter (BIO18), mean temperature of the coldest quarter (BIO11), and temperature seasonality (BIO4) were the main environmental variables influencing the geographical distribution of *I. persulcatus*. According to the response curves, the presence probability of *I. persulcatus* was positively correlated with humidity but negatively correlated with temperature above 0 °C (Supplementary Fig. 4).

As shown in Fig. 6, *I. persulcatus* was predicted to be able to inhabit in the northern hemisphere. Areas with high suitability for *I. persulcatus* were mainly located in the Baltic Sea states (such as Finland, Sweden,

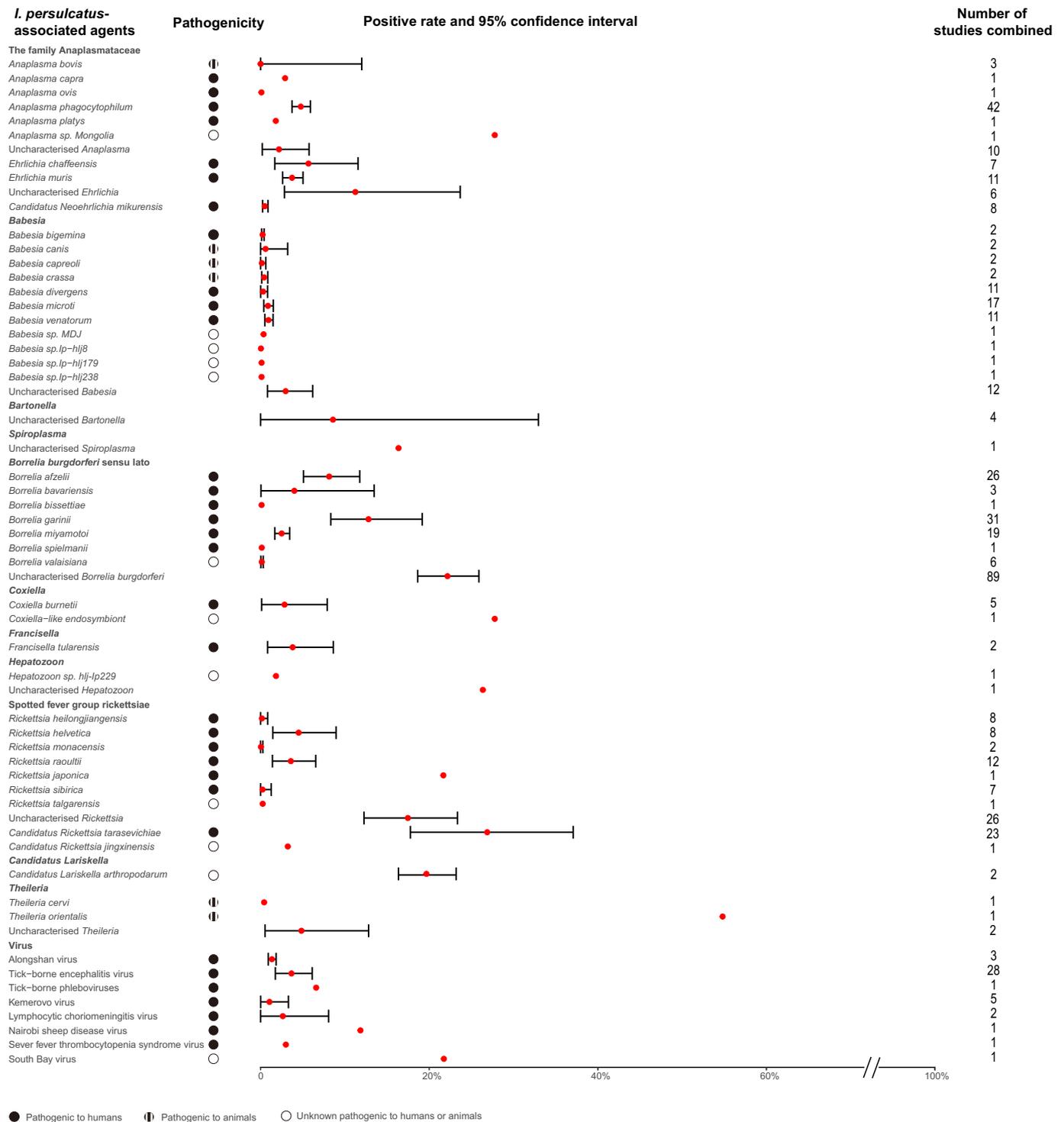


Fig. 4. Prevalence of *I. persulcatus*-associated agents.

Latvia, and Poland); western Russia; northern China; northern Japan; South Korea, and North Korea. Moreover, central and northwestern region of North America, including northern America, southern Canada, and west of Alaska, were also predicted as suitable habitats for *I. persulcatus*. Due to the restriction of ecological factors, the remaining areas of the world were unsuitable for the distribution of the tick species.

4. Discussion

Through the analysis of our integrated database, we found that

I. persulcatus was distributed in 14 countries in the northern hemisphere, parasitized 46 species of hosts, and harbored 51 species of microorganisms. The Maxent model predicted the most suitable habitats for the tick species. The present study provided a comprehensive elaboration of the potential public health risks of *I. persulcatus* and *I. persulcatus*-associated agents in a global scale, facilitating cooperation in multiple fields and departments, and improving monitor, early warning, and control of *I. persulcatus*-borne diseases.

The tick species was reported to distribute between 21° and 66° of north latitude in Eurasia, mostly in areas with a temperate continental



Fig. 5. Geographical distribution of *I. persulcatus*-associated pathogens.

A total of 32 pathogens were carried by *I. persulcatus*. SFTSV=Severe fever with thrombocytopenia syndrome virus.

climate. The adult tick is usually active from early summer to fall. In the southern Russian Far East, the activity phase of the tick may be extended to early November due to the maritime climate [11]. This might be one of the reasons why *I. persulcatus* was widely distributed in Russia. Temperature is the main factor influencing the habitat of the tick species. The life cycle of *I. persulcatus* includes four developmental phases. Its complete development requires that a sum of valid temperatures during the period was no less than 1400 °C, with a stable average temperature surpassing 10 °C [12]. The total of positive temperatures of May and June (above 15 °C) are the basis for consistent tick activity to complete the digestion of blood and nutrient storage [13]. Diapause is a low-temperature adaptation strategy for the tick that helps them survive under unfavorable external conditions and adjust their development and growth accordingly [11]. Besides, precipitation parameters in combination with thermal regime have considerable influence on *I. persulcatus* activity [14]. Also, the vegetation has an impact on the tick distribution to some extent. *I. persulcatus* prefers wetted biotopes with small open areas to high-mountainous area without large forests, reaching its maximum abundance in the subzone of mixed forest [15–17].

I. persulcatus was collected on 46 different host species according to our study, showing a wide host range and good adaptability. The tick species is a typical three-host species [11]. Larvae of *I. persulcatus* feed mainly on small mammals, nymphs feed on small and medium-sized mammals, and adults seek medium to large-sized hosts [18]. Notably, a total of 21 species of animals are found only in Russia, involving birds and rodents, indicating a higher risk of zoonosis.

Canis lupus (dog), as a significant host of *I. persulcatus*, was reported

to be parasitized by the tick species by 5 countries. Due to their ubiquitous social interactions with human and widespread distribution, dog owners should raise awareness of preventing dogs from tick infestation; and measures should be taken to control tick-borne diseases in dogs, which might affect people in contact. Various birds, especially migratory birds, are potential disseminators of TBEV and *Borrelia* spp., and may play a more important role in the transmission of ticks and associated pathogens to remote areas than small feral rodents [19–22]. *Riparia riparia*, one of the animal hosts of *I. persulcatus* in Russia, migrates to Africa in winter [19]. *Turdus pilaris*, which is widely distributed in Europe, northern Asia, and Africa, typically winters in West and South Europe and Southwest Asia [23]. The migratory behavior of birds may bring a great risk of tick-borne infections to new biotopes on specific migration routes. It is imperative to establish a tick-borne pathogen surveillance network in birds and to conduct dynamic epidemiological surveys to confirm the role of wild birds in disease spread.

I. persulcatus could carry 33 human pathogens, of which CRT had the highest prevalence at 26.88% (95%CI 17.77–37.08). *I. persulcatus* constitutes the main vector of CRT in Europe and Asia, and there exists an efficient transovarial transmission of this bacteria in the tick species [24]. *A. phagocytophilum*, a zoonotic bacterium that replicates in neutrophil granulocytes and elicits febrile disease in humans and animals [25], is the most reported pathogen in *I. persulcatus*, and mainly distributed in Russia and China. At present, Lyme disease is the most common tick-borne zoonosis in temperate regions of the northern hemisphere [18]. In Eurasia, *B. afzelii* and *B. garinii*, carried by *I. persulcatus*, are the main causative agents for the disease. *B. afzelii*

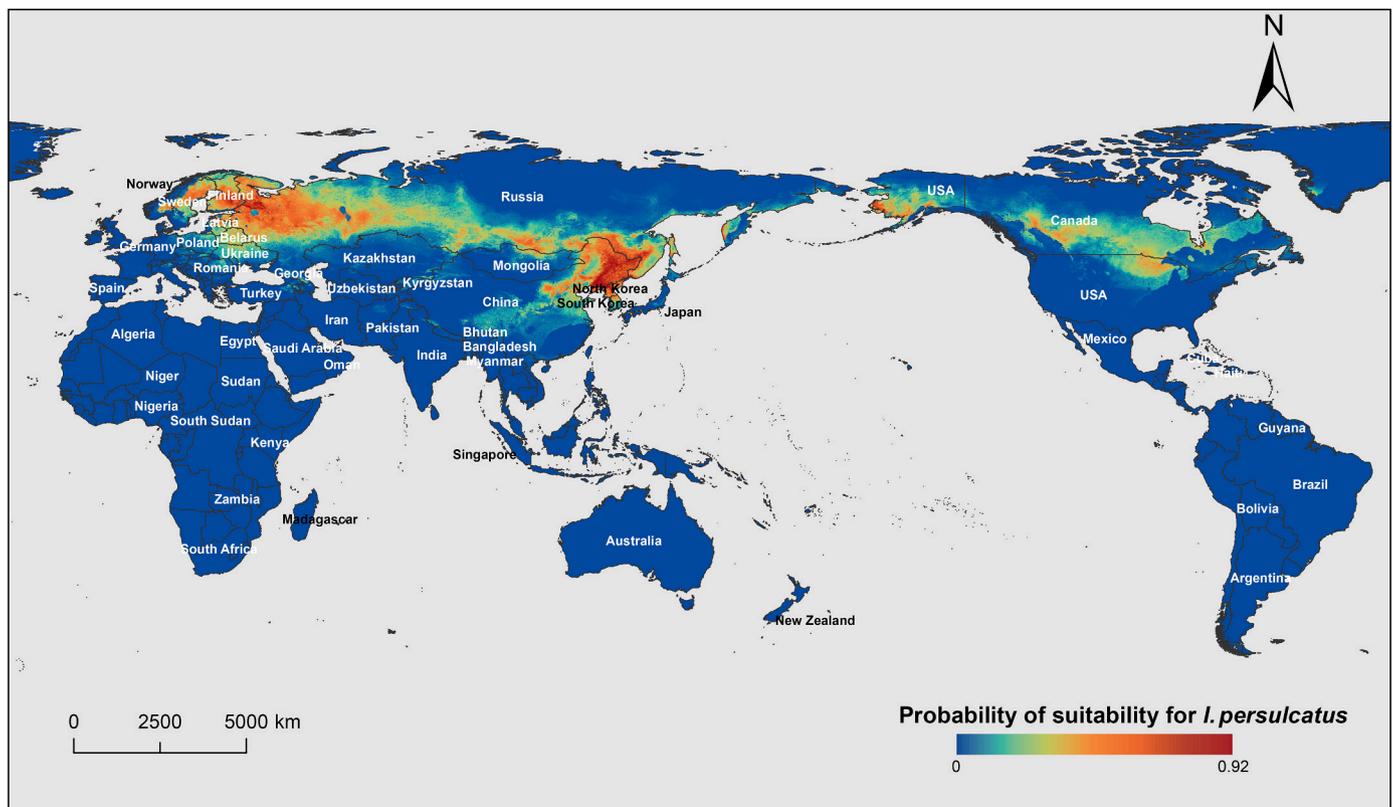


Fig. 6. Potential distribution map of *I. persulcatus* globally. Predicted probability of *I. persulcatus* occurrence are displayed on the backgrounds of Maxent-created ecological niche model.

primarily cause skin infection, while *B. garinii* is most commonly associated with neuroborreliosis. Tick-borne encephalitis is the most significant flavivirus infection involving central nervous system in Eurasia, which has been listed as a notifiable disease in the European Union since 2012 [26,27]. There are three major subtypes of TBEV, of which the FE and Sib subtypes are mainly transmitted by *I. persulcatus* in western Europe and may lead to severe encephalitic symptoms or chronic infections [26,28]. With the changes of climate and environmental conditions, the expanding range of *I. persulcatus* and the increasing incidence of tick-borne encephalitis have become a growing problem [29]. Numerous emerging pathogens of public health concerns like Alongshan virus are also closely related to the tick species [30]. Therefore, more surveillance and investigations of *I. persulcatus* and associated pathogens are required to reduce the burden of tick-borne diseases.

For now, studies predicting suitable habitats of *I. persulcatus* are particularly limited. In our model, BIO18, BIO11, BIO4, and BIO19 were major factors that contribute more than 80% of the model under current climate conditions. And the model shows that the distribution of the tick species was mainly determined by temperature and humidity. High temperature in the driest quarter was associated with a low probability of presence for *I. persulcatus* based on BRT models [31], indicating that low temperature is more suitable for the tick species. According to previous studies, the highly suitable habitats of *I. persulcatus* were predominantly located in northeastern China [32], which is consistent with our results. However, the prediction map in our study revealed that *I. persulcatus* might be able to inhabit more extensive areas than previously recorded, such as North America, where no available evidence with this tick species exists. In this area, two close relatives of *I. persulcatus*, *Ixodes scapularis* and *Ixodes pacificus*, were identified, all three of which belong to the *Ixodes ricinus* species complex and show high similarity in morphological and ecological features [11,33–35]. Further explorations and monitoring programs are needed to confirm

the presence of *I. persulcatus* in the future. Tick distribution models can be used to predict where tick-borne infections might emerge in the absence of a thorough pathogen monitoring program [36]. Therefore, our results could be utilized to conduct control and management programs against *I. persulcatus* and to help identifying the emerging risk of *I. persulcatus*-borne diseases in an endemic area.

There are several shortcomings in our study that should be pointed out. First, publication limitation could have been present due to the inclusion of only English and Chinese published studies. Second, detection methods, reagents, and sensitivities vary by research period, area, and design. Poor identification of some tick-borne pathogens in earlier published studies may result in a lack of detailed information about distribution or prevalence of the related pathogens in some areas. And full repertoire of the tick-borne pathogens should be assessed by large-scale metagenomic and transcriptomic studies.

5. Conclusion

In summary, *I. persulcatus* inhabits in a variety of countries of Eurasia, feeds on multiple hosts, and harbors various pathogens, which is a great public health concern. The predictive model demonstrates that the tick species is suitable to distribute in more extensive areas. An efficient tick-surveillance network should be enhanced to mitigate *I. persulcatus* and *I. persulcatus*-borne diseases. Multi-country and multi-department collaborations should be strengthened to promote the health of humans, animals, and ecosystems through communication, information-sharing, and group decision-making. Our study yields a new clue for clarifying the key points to control the outbreak of tick-borne diseases, and identifying where to implement tick surveillance strategies on a wider range.

Authorship contributions

WCC and LZ conceived and designed the study. WBG, JFJ, XMC, YSP, YHZ, BGJ, and ZTL did the field survey. SSW and JYL collected the data. SSW, BYW, and WJW did the data analysis. YS provided data for the reference book and identified the tick samples. WCC, LZ, and SSW interpreted the results. LZ and SSW wrote the manuscript, and WC and LZ revised the manuscript. All authors contributed substantially to data acquisition and interpretation, and revision and editing of the manuscript.

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Declaration of Competing Interest

We declare no competing interests.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.onehlt.2023.100508>.

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