Preplanned Studies

Niche Analysis of Spatial Distribution and Host Selection of Global *Echinococcus* Species — Worldwide, up to June 30, 2024

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Summary

What is already known about this topic?

Echinococcosis is a serious public health concern caused by *Echinococcus* larvae. To date, 10 *Echinococcus* species have been identified globally, each with potential variations in geographic distribution and host selection.

What is added by this report?

This study presented the provincial-level distribution of all *Echinococcus* species globally and constructed a host frequency matrix for them. By quantifying both spatial and host niches, it provides comprehensive data for understanding the ecological adaptability of *Echinococcus* species and the transmission patterns of echinococcosis.

What are the implications for public health practice?

This study's results highlight the interspecific heterogeneity and associations among different *Echinococcus* species, suggesting the need for targeted approaches in epidemiological investigations, source tracing, and risk surveillance to effectively control echinococcosis.

ABSTRACT

Objective: Echinococcosis is a fatal parasitic disease caused by infection with the larval stages of *Echinococcus* spp.. This study explored the spatial distribution characteristics and the host selection patterns of global *Echinococcus* species based on niche analysis, to provide scientific insights for the prevention and control of echinococcosis.

Methods: Relevant literature was retrieved from Web of Science, PubMed, ScienceDirect, and CNKI (China National Knowledge Infrastructure) databases. Data on the host information and geographic locations for all *Echinococcus* species worldwide were extracted. The spatial distribution characteristics of *Echinococcus* were summarized, and the host frequency heatmaps were generated using the SRplot platform. Niche indices were calculated and visualized using R language packages and the Hiplot Pro platform.

Results: The ten existing *Echinococcus* species were documented across 1,770 provincial-level administrative divisions in 113 countries, involving 188 species of host animals. Significant heterogeneity with varying degrees of overlap and differentiation was observed in spatial and host niches among *Echinococcus* species. The overall spatial distribution among *Echinococcus* species showed a significantly negative correlation (VR=0.85, W=1,502.79<χ^2 0.951770), while host selection patterns revealed no significant correlation (VR=0.90, χ^2 0.95187<W=167.70<χ^2 0.05187). *Echinococcus granulosus* and *Echinococcus multilocularis* exhibited the broadest spatial niche (B_{Eg}=7.34) and host niche (B_{Em}=3.07), respectively.

Conclusion: The spatial distribution and host selection among *Echinococcus* species exhibit complex heterogeneity and correlations, requiring the development of targeted strategies for the prevention, control, and surveillance of echinococcosis.

Echinococcosis is a deadly infectious disease caused by *Echinococcus* larvae infection (*1*). Understanding the ecological niche of *Echinococcus* is crucial for exploring echinococcosis epidemiology. This study retrieved infection events and investigations of all 10 *Echinococcus* species from databases and found that *Echinococcus* spp. are currently distributed in at least 1,770 provincial regions across 113 countries, with 188 mammalian host species globally. Significant heterogeneity exists in the geographical distribution and host selection among different *Echinococcus* species. The niche overlap and separation of *Echinococcus* species contribute to the complexity, diversification, and endemicity of echinococcosis. These findings suggest that current surveillance approaches should be reconsidered and that differences among *Echinococcus* species must be fully accounted for in echinococcosis control. Specific host surveillance, targeted control strategies, and precise epidemiological investigations should be tailored to different types of endemic areas.

Echinococcosis causes approximately 19,300 deaths and 871,000 disability-adjusted life years, and costs more than 3 billion United States Dollars (USD) worldwide per year (*2*). Recent studies have recognized 10 valid natural species of *Echinococcus* worldwide: *Echinococcus granulosus* (*Eg*), *E. equinus* (*Ee*), *E. ortleppi* (*Eor*), *E. intermedius* (*Ei*), *E. canadensis* (*Ec*), *E. felidis* (*Ef*), *E. multilocularis* (*Em*), *E. shiquicus* (*Es*), *E. vogeli* (*Ev*), and *E. oligarthra* (*Eol*) (*1*). Host suitability and geographical distribution vary significantly among these *Echinococcus* species; however, detailed information remains limited due to a lack of systematic molecular data (*3*).

In this study, researchers conducted a comprehensive literature search from the Web of Science (https://webofscience.clarivate.cn), PubMed (https://pubmed.ncbi.nlm.nih.gov), ScienceDirect (https://www.sciencedirect.com/), and the China National Knowledge Infrastructure (https://www.cnki.net/) databases using the search terms "*Echinococcus*," "echinococcosis," "hydatid disease," and "hydatidosis." The final search was completed on June 30, 2024. This study's authors performed full-text reviews and included articles with detailed investigation locations and clear identification of *Echinococcus* species/genotypes or echinococcosis types. Data on *Echinococcus* species, host species, and discovery locations (provincial-level administrative divisions, PLADs) were then extracted for subsequent analyses. The heat map of host occurrence frequencies was generated using the SRplot platform (https://www.bioinformatics.com.cn). Four ecological indices were calculated and visualized using the spaa package in R version 4.1.3 (R Core Team, Vienna, Austria) and Hiplot Pro platform (https://hiplot.com.cn): Shannon's niche width (breadth) index (B_i), Levin's niche overlap index ($O_{i\text{-}k}$), the overall interspecific association quantified by the variance ratio (VR) and tested for significance using the statistic W, and interspecific association coefficient (AC).

According to globally available data from 285 formal publications, 10 *Echinococcus* species have been reported in 1,770 provincial administrations across 113 countries (34 in Asia, 41 in Europe, 21 in Africa, 5 in North America, 11 in South America, and 1 in Oceania) (Supplementary Material, available at https://weekly.chinacdc.cn/). *Echinococcus* spp. have been observed or detected in 188 host species from 25 families, comprising 157 species (94 rodents, 34 ungulates, 18 marsupials, 7 primates, and 4 insectivores) serving as intermediate hosts (IHs) and 30 species (17 canids, 12 felids, and 1 quoll) acting as definitive hosts (DHs). Humans are considered accidental hosts and play a dead-end role in the life cycle of *Echinococcus* spp. (Figure 1).

Among the 10 *Echinococcus* species, *Eg* was the most extensively documented across 93 countries (Asia, Europe, Africa, Oceania and the Americas), with dogs serving as the primary DHs (95.52% of all DH occurrences) and Bovidae animals as the predominant IHs (89.81% of all IH occurrences). *Em* was identified in 58 countries (Asia, Europe and North America), with foxes (47.26%) and dogs (35.98%) as the main DHs, and rodents as the principal IHs (93.83%). *Ei* was reported in 52 countries (Asia, Europe, Africa and South America), with dogs (61.29%) as the primary DHs, and camels (26.12%) and pigs (22.39%) as the main IHs. *Eor* was found in 35 countries (Asia, Europe, Africa and Latin America), with dogs (75.00%) as the predominant DHs, and cattle (57.89%) and pigs (11.58%) as the main IHs. *Ec* was identified in 10 countries in northern Asia, Europe and North America, with wolves (78.95%) and coyotes (21.05%) as DHs and Cervidae animals (96.43%) as IHs. *Ee* was recorded in 17 countries (western and southern Europe, western and central Asia, eastern and southern Africa), with dogs (60.00%) as the main DHs and Equidae animals (75.76%) as the principal IHs. *Ev* was documented in 10 countries in northern South America, with *Speothos venaticus* (85.71%) and *Cuniculus paca* (63.64%) being the main DH and IH, respectively. *Eol* was recorded in 8 countries in Latin America, with agouties (54.55%) as the main IHs and *Puma concolor* (33.33%) and other American Feline animals as the DHs. *Ef* was found in 5 countries (Kenya, Namibia, Uganda, Zambia and South Africa) in Sub-Saharan Africa, with lions (73.33%) being the preferred DHs, and warthogs and hippopotamuses as the few documented IHs. *Es* is currently considered endemic to the Tibetan Plateau in China, with *Ochotona curzoniae* (66.67%) and *Vulpes ferrilata* (42.86%) being the main IH and DH, respectively. Additionally, the most frequent cause of human echinococcosis was *Eg* (69.45%), followed by *Em* (10.24%), *Ei* (9.04%), *Eor* (4.78%), *Ev* (3.75%), *Eol* (1.19%), *Ec* (0.85%), and *Ee* (0.68%), whereas *Es* and

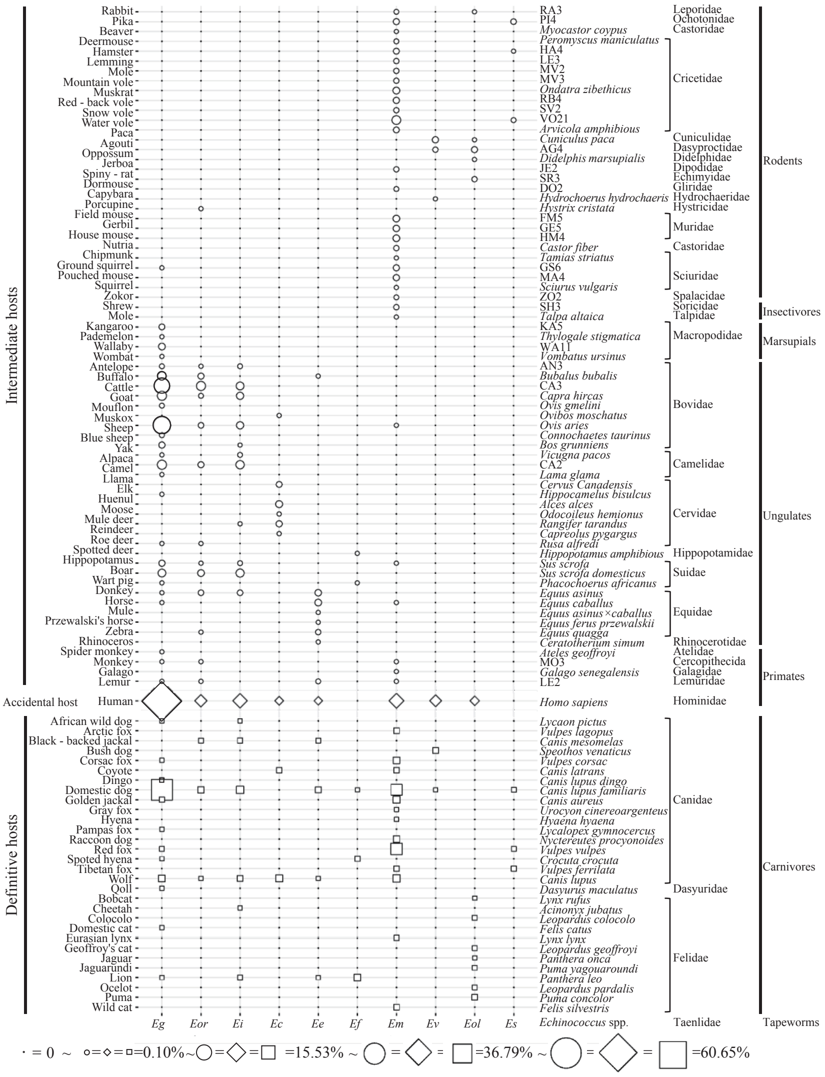

FIGURE 1. The heatmap for host occurrence frequencies of 10 *Echinococcus* species.

Note: A separate information pool was created for each *Echinococcus* species, encompassing all reported host species within each provincial district (with each host species recorded only once per PLAD). The statistics for intermediate hosts, definitive hosts, and humans within each information pool were treated independently. Occurrence frequency = (the number of occurrences of the species/the total number of occurrences of all species recorded in the information pool) × 100%. RA3: *L. europaeus*, *L. oiostolus*, *Sylvilagus floridanus*; PI4: *Ochotona dauurica*, *O. pallasii*, *O. rufescens*, *O. curzoniae*; HA4: *Cricetulus barabensis*, *C. kamensis*, *C. migratorius*, *C. longicaudatus*; LE3: *Lemmus lemmus*, *L. sibiricus*, *Dicrostonyx torquatus*; MV2: *Ellobius talpinus*, *E. tancrei*; MV3: *Alticola argentatus*, *A. olchonensis*, *A. strelzovi*; RB4: *Myodes rutilus*, *M. rex*, *M. rufocanus*, *Clethrionomys gapperi*; SV2: *Chionomys nivalis*, *C. roberti*; VO21: *Alexandromys limnophilus*, *A. middendorffii*, *A. oeconomus*, *Blanfordimys juldaschi*, *Lagurus lagurus*, *Lasiopodomys brandtii*, *L. gregalis*, *Microtus agrestis*, *M. arvalis*, *M. guentheri*, *M. ilaeus*, *M. irani*, *M. mystacinus*, *M. pennsylvanicus*, *M. socialis*, *M. subterraneus*, *M. transcaspicus*, *Myodes glareolus*, *Neodon irene*, *N. leucurus*, *N. fuscus*; AG4: *Dasyprocta leporina*, *D. azarae*, *D. punctata*, *D. fuliginosa*; JE2: *Pygeretmus pumilio*, *Scarturus elater*; SR3: *Proechimys guyannensis*, *P. trinitatus*, *P. semispinosus*; DO2: *Dryomys nitedula*, *Eliomys quercinus*; FM5: *Apodemus agrarius*, *A. argenteus*, *A. sylvaticus*, *A. uralensis*, *A. witherbyi*; GE5: *Meriones libycus*, *M. meridianus*, *M. persicus*, *M. unguiculatus*, *Rhombomys opimus*; HM4: *Mus macedonicus*, *M. musculus*, *Nesokia indica*, *Rattus norvegicus*; GS6: *Spermophilus alashanicus*, *S. erythrogenys*, *S. pygmaeus*, S. relictus, *Urocitellus undulates*. MA4: *Marmota baibacina*, *M. bobak*, *M. caudata*, *M. marmota*; ZO2: *Eospalax fontanierii*, *Myospalax myospalax*. SH3: *Sorex unguiculatus*, *S. jacksoni*, *Crocidura suaveolens*; KA5: *Macropus giganteus*, *M. rufogriseus*, *M. fuliginosus*, *M. dorsalis*, *Dendrolagus lumholtzi*; WA11: *Macropus parryi*, *Notamacropus dorsalis*, *N. parryi*, *N. rufogriseus*, *Onychogalea fraenata*, *Osphranter robustus*, *Petrogale godmani*, *P. mareeba*, *P. penicillata*, *P. persephone*, *Wallabia bicolor*; AN3: *Addax nasomaculatus*, *Gazella gazelle*, *Oryx gazelle*; CA3: *Bos taurus*, *B. indicus*, *B. frontalis*; CA2: *Camelus dromedaries*, *C. bactrianus*; MO3: *Cercopithecus ascanius*, *Pygathrix nemaeus*, *Macaca sylvanus*; LE2: *Lemur catta*, *Varecia rubra*.

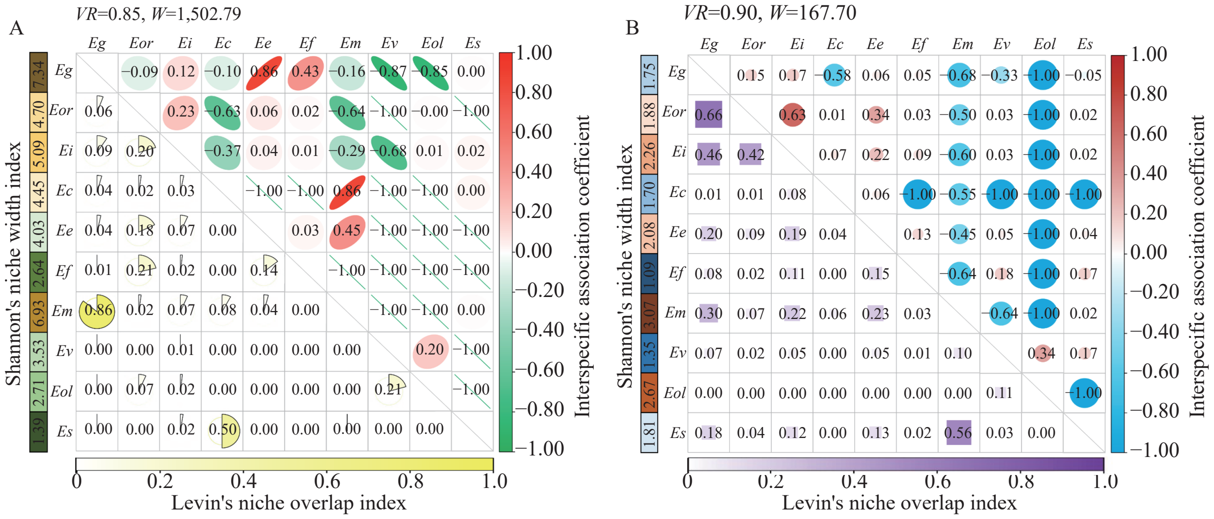

FIGURE 2. The spatial and host niche indexes of 10 *Echinococcus* species. (A) the spatial niche indexes; (B) the host niche indexes.

Note: Shannon's niche width (breadth) index (B_i)=$-\sum_{j=1}^{N}(P_{ij}\times \mathrm{Ln}P_{ij})$; Levin's niche overlap index (O_{ik})=$\frac{\sum_{j=1}^{N}(P_{ij}\times P_{kj})}{\sum_{j=1}^{N}(P_{ij})^2}$; variance ratio (*VR*)=$\frac{1/N\sum_{j=1}^{N}(T_j-t)^2}{\sum_{i=1}^{s}[(n_i/N)\times(1-n_i/N)]}$; Statistic *W*=*VR***N*; interspecific association coefficient (*AC*)=$\frac{a\times d-b\times c}{(a+b)\times(b+d)}$ (if $a*d \geq b*c$) or $\frac{a\times d-b\times c}{(a+b)\times(a+c)}$ (if $a*d < b*c$ and $a \leq d$) or $\frac{a\times d-b\times c}{(b+d)\times(d+c)}$ (if $a*d < b*c$ and $a > d$); *i* and *k* represents the *Echinococcus* species (*i*) and (*k*), respectively; *j* represents the space (PLAD) (*j*) or host species (*j*); *N* represents the number of spaces (PLADs) or host species; P_{ij} and P_{kj} represents abundance of species (*i*) and (*k*) for (*j*), respectively; *S* represents the number of *Echinococcus* species; n_i represents the number of spaces (PLADs) or host species that (*i*) appears; T_j represents the number of *Echinococcus* species for (*j*); *t* represents the mean number of *Echinococcus* species for all spaces (PLADs) or host species; *a* represents the number of spaces (PLADs) or host species occupied both by (*i*) and (*k*); *b* represents the number of spaces (PLADs) or host species occupied only by (*i*); *c* represents the number of spaces (PLADs) or host species only have (*k*); *d* represents the number of spaces (PLADs) or host species without (*i*) or (*k*); B_i represents the niche width of species (*i*), with a higher value indicating a wider niche; O_{ik} denotes the index of niche overlap between *Echinococcus* species of (*i*) and (*k*), with a higher value indicating more niche overlap; *VR* refers variance ratio of the number to the relative frequency of *Echinococcus* species, with a value >1 indicating a positive overall interspecific association and a value <1 indicating negative association; *W* is used in comparison with chi square (χ^2) threshold with *N*, with a value $>\chi^2$ (P=0.05) or χ^2 (P=0.95) indicating a significant overall interspecific association and a value $<\chi^2$ (P=0.05) and $>\chi^2$ (P=0.95) indicating an insignificant association; *AC* represents interspecific association between each pair of species, with a value >1 indicating a positive association and a value <1 indicating negative association.
Abbreviation: PLAD=provincial-level administrative division.

Ef have not yet been recorded in humans (Figure 1 and Supplementary Material).

In terms of the spatial niche, *Eg* exhibited the largest niche width (B_{Eg}=7.34), with niche overlap with nearly all other species (mean $O_{Eg\text{-}others}$=0.12±0.28), particularly with *Em* ($O_{Eg\text{-}Em}$=0.86). Conversely, the niche overlaps between *Ev* and other species were the lowest ($O_{mean\text{-}Ev}$=0.02±0.06), and *Es* showed the smallest niche width (B_{Es}=1.39). For the host (excluding humans) niche, *Em* had the largest niche width (B_{Em}=3.07), whereas *Ef* had the smallest niche width (B_{Ef}=0.03). The group comprising *Eg*, *Eor*, and *Ei* (mean $O_{Eg\text{-}Eor\text{-}Ei}$=0.64±0.04) and that comprising *Em* and *Es* ($O_{Em\text{-}Es}$=0.56) exhibited higher niche overlaps. The overall interspecific association of spatial distribution among *Echinococcus* species (*VR*=0.85, *W*=1,502.79) showed significant negative associations, with 14 (*AC*>0) and 31 (*AC*<0) pairs of positive and negative correlations, respectively, in all interspecific correlations. The overall interspecific association of host selection (*VR*=0.90, *W*=167.70) showed no significant associations, with 16 positive and 29 negative pairs (Figure 2).

To date, human echinococcosis caused by *Eg*, *Em*, *Ei*, *Ec*, and *Eor* has been identified in China. These findings will facilitate the development of targeted, differentiated, and localized control and surveillance strategies to address the complex epidemiology of echinococcosis.

DISCUSSION

Notably, *Eg* is the most common cause of cystic echinococcosis (CE) globally, followed by *Ei*, which also has a widespread global distribution. Additionally, *Eor*, *Ec*, and *Ee* can cause endemic CE. *Eor* is primarily concentrated in the tropical and subtropical regions, *Ec* is mainly distributed in the frigid and sub-frigid zones, and *Ee* is more common in the temperate and tropical grasslands. Furthermore, *Em* causes alveolar echinococcosis (AE) in the Northern Hemisphere, while *Ev* and *Eol* cause polycystic and unicystic echinococcosis, respectively, in the neotropical regions. *Ef* and *Es* are confined to sub-Saharan Africa and the Tibetan Plateau in China, respectively (*4*). The significant negative association in spatial distribution suggests the existence of interspecific competition or differentiation for habitat utilization among different *Echinococcus* species.

The main intermediate hosts of *Eg*, *Ei*, and *Eor* are Bovidae, Camelidae, and Suidae; however, *Eg* is also susceptible to marsupials, and both *Eg* and *Eor* can infect primates. *Ec* and *Ee* prefer Cervicidae and Equidae as intermediate hosts, respectively. Interestingly, the definitive hosts of *Ec* have only been recorded in wild canids (wolves and coyotes), whereas *Ee* has been found in both domestic and wild canids (dogs, wolves, and jackals). The intermediate hosts of *Em*, *Es*, *Ev*, and *Eol* are mainly native rodents from Eurasia, the Tibetan Plateau, South America, and Latin America, respectively. *Em*, *Es*, *Ec*, *Ef*, and *Eol* are the five species that can complete their life cycles through predation by wild animals, with *Ec*, *Ef*, and *Eol* even capable of parasitizing exclusively in wildlife. Additionally, *Ef* and *Eol* rely on feline animals as their primary definitive hosts for transmission (*5*). Dog infections have not been recorded for *Ec* and *Eol*. This study's results demonstrate a relatively independent host selection pattern with loose interspecific association among the different *Echinococcus* species.

Notably, *Eg* had the widest spatial niche, indicating its exceptional adaptability to diverse habitats. It is found on almost all continents inhabited by humans and represents the dominant pathogen causing human echinococcosis, primarily due to its main hosts (dogs and livestock) which can migrate globally with human activities. However, a disadvantage of its host niche is that the transmission chain of *Eg* is relatively fragile. Interventions targeting dog infections or improving livestock slaughter management can effectively contain CE epidemics caused by *Eg*. In contrast, *Em* demonstrates a significant advantage in host niche breadth, revealing a highly complex lifecycle involving numerous host species, particularly wildlife. Consequently, AE caused by *Em* exhibits diverse and unpredictable transmission pathways, posing substantial challenges to disease control efforts (*6*).

However, limitations in development level, technical capabilities, and research priorities have resulted in many countries and regions lacking comprehensive surveillance systems for echinococcosis and molecular data on *Echinococcus* species, making it difficult to determine the actual prevalence of this zoonotic disease in detail (*7*). In particular, this study cannot definitively establish the presence or absence of *Echinococcus* species in areas without confirmed research. Therefore, in this study, its authors focused on distribution at intercontinental geographical scales and climatic zone levels, using maximum boundaries to describe the spatial characteristics of *Echinococcus*.

This study highlights the need for adaptive adjustments to surveillance and control programs based on local echinococcosis epidemiology. For example, host surveillance for CE caused by *Eor* in southwest China (Yunnan, Guangxi, and Guizhou) should equally consider pigs in addition to cattle (*8*). Regarding the emergence of *Ec*-induced CE in northeast China (Heilongjiang), surveillance of local deer and wolves for *Echinococcus* infection should be implemented (*9*), whereas for *Ei*-induced CE occurring in northwest China (Xinjiang and Inner Mongolia), infection surveillance in camels is warranted (*10*). Furthermore, *Ee*-induced CE, prevalent in Central Asia (Kyrgyzstan) and posing a pathogenic threat to humans, necessitates surveillance of Equidae animals (horses and donkeys) in neighboring areas of China (Xinjiang).

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SUPPLEMENTARY MATERIAL

List of Countries and Regions where *Echinococcus* species have been Reported

Echinococcus granulosus:

Afghanistan, Albania, Algeria, Argentina, Armenia, Australia, Austria, Azerbaijan, Bahrain, Bangladesh, Belgium, Bhutan, Bolivia, Bosnia and Herzegovina, Brazil, Bulgaria, Chile, China, Croatia, Cyprus, Czech Republic, Egypt, Estonia, Ethiopia, Finland, France, Georgia, Germany, Greece, Hungary, Iceland, India, Indonesia, Iran, Iraq, Ireland, Israel, Italy, Jordan, Kazakhstan, Kenya, Kosovo, Kuwait, Kyrgyzstan, Latvia, Lebanon, Libya, Lithuania, Luxembourg, North Macedonia, Malta, Mauritania, Mexico, Moldova, Mongolia, Montenegro, Morocco, Namibia, Nepal, Nigeria, Norway, Oman, Pakistan, Palestine, Peru, Poland, Portugal, Qatar, Romania, Russia, Saudi Arabia, Serbia, Slovakia, Slovenia, South Africa, Spain, Sudan, Sweden, Switzerland, Syria, Tajikistan, Tanzania, Tunisia, Turkey, Turkmenistan, Uganda, UK, Ukraine, Uruguay, Uzbekistan, Vietnam, Yemen.

E. multilocularis:

Afghanistan, Albania, Armenia, Austria, Azerbaijan, Belgium, Bosnia and Herzegovina, Bulgaria, Canada, China, Croatia, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Georgia, Germany, Greece, Hungary, Iran, Iraq, Ireland, Italy, Japan, Kazakhstan, Kosovo, Kyrgyzstan, Latvia, Liechtenstein, Lithuania, Luxembourg, North Macedonia, Malta, Mongolia, Montenegro, Netherlands, Norway, Pakistan, Poland, Portugal, Romania, Russia, Serbia, Slovakia, Slovenia, South Korea, Spain, Sweden, Switzerland, Tajikistan, Turkey, Turkmenistan, UK, Ukraine, USA, Uzbekistan.

E. intermedius:

Afghanistan, Algeria, Argentina, Austria, Bolivia, Brazil, Cape Verde, Chile, China, Ecuador, Egypt, Ethiopia, France, Ghana, Greece, Hungary, India, Iran, Italy, Kazakhstan, Kenya, Libya, Lithuania, Mali, Mauritania, Mexico, Moldova, Mongolia, Namibia, Nigeria, Oman, Pakistan, Peru, Poland, Portugal, Romania, Russia, Saudi Arabia, Serbia, Slovakia, Slovenia, Somalia, South Africa, Spain, Sudan, Tanzania, Tunisia, Turkey, Uganda, Ukraine, Zambia.

E. ortleppi:

Argentina, Bhutan, Bolivia, Bosnia and Herzegovina, Brazil, Chile, China, Egypt, Ethiopia, France, Germany, India, Iran, Italy, Kenya, Mexico, Mozambique, Namibia, Nepal, Netherlands, Pakistan, Poland, Portugal, Saudi Arabia, Serbia, South Africa, South Sudan, Sudan, Switzerland, Tanzania, Turkey, UK, Uruguay, Vietnam, Zambia.

E. equinus:

Canada, Chile, Egypt, Ethiopia, Germany, Ireland, Italy, Kenya, Kyrgyzstan, Namibia, Pakistan, South Africa, Spain, Tunisia, Turkey, UK, Uzbekistan.

E. canadensis:

Canada, China, Estonia, Finland, Latvia, Mongolia, Poland, Russia, Sweden, USA.

E. vogeli:

Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, Panama, Peru, Suriname, Venezuela.

E. oligarthra:

Argentina, Brazil, Colombia, Costa Rica, Mexico, Panama, Suriname, Venezuela.

E. felidis:

Kenya, Namibia, South Africa, Uganda, Zambia.

E. shiquicus:

China.