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Review

Echinococcosis in wild carnivorous species: Epidemiology, genotypic diversity, and implications for veterinary public health

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ABSTRACT

Echinococcosis is a zoonosis caused by helminths of the genus *Echinococcus*. The infection, one of the 17 neglected tropical diseases listed by the World Health Organization, has a cosmopolitan distribution and can be transmitted through a variety of domestic, synanthropic, and sylvatic cycles. Wildlife has been increasingly regarded as a relevant source of infection to humans, as demonstrated by the fact that a significant proportion of human emerging infectious diseases have a wildlife origin. Based on available epidemiological and molecular evidence, of the nine *Echinococcus* species currently recognized as valid taxa, *E. canadensis* G8–G10, *E. felidis*, *E. multilocularis*, *E. oligarthrus*, *E. shiquicus*, and *E. vogeli* are primarily transmitted in the wild. *E. canadensis* G6–G7, *E. equinus*, *E. granulosus* s.s., and *E. ortleppi* are considered to be transmitted mainly through domestic cycles. We summarize here current knowledge on the global epidemiology, geographical distribution and genotype frequency of *Echinococcus* spp. in wild carnivorous species. Topics addressed include the significance of the wildlife/livestock/human interface, the sympatric occurrence of different *Echinococcus* species in a given epidemiological scenario, and the role of wildlife as natural reservoir of disease to human and domestic animal populations. We have also discussed the impact that human activity and intervention may cause in the transmission dynamics of echinococcosis, including the human population expansion and encroachment on shrinking natural habitats, the increasing urbanization of wildlife carnivorous species and the related establishment of synanthropic cycles of *Echinococcus* spp., the land use (e.g. deforestation and agricultural practices), and the unsupervised international trade and translocation of wildlife animals. Following the 'One Health' approach, we have also emphasized that successful veterinary public health interventions in the field of echinococcosis requires an holistic approach to integrate current knowledge on human medicine, veterinary medicine and environmental sciences.

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1. Introduction

Zoonoses are defined as infectious diseases that are naturally transmitted between vertebrate animal species and humans (WHO, 1951). Overall, 61% (868/1415) of the species of infectious organisms known to be pathogenic to humans are zoonotic (Taylor et al., 2001). Among them, helminths are especially likely to be associated with zoonoses, as 95% (274/287) of the members of this parasite group have wild and/or domestic animals acting as natural reservoirs (Taylor et al., 2001). Furthermore, 60% of human emerging infectious diseases can also be catalogued as zoonoses, the majority of these (71.8%) being originated in wildlife (Jones et al., 2008). Not surprisingly, wildlife has received increasing attention in recent years not only as potential reservoir of disease to domestic animals and humans (Kruse et al., 2004; Chomel et al., 2007), but also as recipient of pathogenic agents resulting from spill-over from domestic hosts (Thompson, 2013). This scenario has contributed to the establishment of the “One Health” concept, which has been defined as ‘the collaborative effort of multiple disciplines—working locally, nationally, and globally—to attain optimal health for people, animals and the environment’ (American Veterinary Medical Association, 2008). Under this approach, animal and environmental health is thought to be mutual and dynamically intersected, and therefore should be considered as a whole (Alexander et al., 2012; Thompson, 2013). Characterization of zoonotic disease transmission with a wildlife reservoir is a complex task which is usually hindered by limited knowledge regarding pathogen diversity and susceptibility (MacPhee and Greenwood, 2013). In addition, a number of natural (size and density of wildlife host populations) or anthropogenic (human population expansion and encroachment,

changes in agricultural practices, reforestation, wildlife translocation, and climatic changes) factors may have a marked influence on the epidemiology of these zoonoses (Kruse et al., 2004; Chomel et al., 2007).

Members of the genus *Echinococcus* are zoonotic helminth parasites (phylum Platyhelminthes, class Cestoda) with a worldwide distribution. The adult worm lives in the small intestine of suitable canids (domestic and bush dogs, wolves, foxes, jackals, racoon dogs, and coyotes), felids (lions, cougars, jaguars, and jaguarundis), and hyenids (hyenas) laying eggs that are excreted with the faeces of the animal and contaminating the environment. Susceptible intermediate host (ungulate and rodent) species that accidentally ingest infective eggs will develop the parasite’s larval stage or metacestode. Humans are an aberrant, dead-end host that do not play a role in the natural cycle of the parasite. Based on recent molecular and phylogenetic evidence, the *Echinococcus* genus comprises nine valid species including *E. granulosus* sensu stricto (*E. granulosus* s.s., genotypes G1–G3), *E. equinus* (G4), *E. ortleppi* (G5), *E. canadensis* (G6–G10), *E. felidis*, *E. multilocularis*, *E. oligarthrus*, *E. shiquicus*, and *E. vogeli* (Thompson and McManus, 2002; Xiao et al., 2005; Nakao et al., 2007, 2013a,b; Huttner et al., 2008; Thompson, 2008). In addition, intraspecific phylogeny and geographical variations have also been reported in *E. multilocularis* and the Neotropical species *E. vogeli* (Knapp et al., 2009; Nakao et al., 2009; Santos et al., 2012).

E. granulosus s.s., *E. equinus*, and *E. ortleppi* are essentially maintained in domestic cycles involving dogs and a number of livestock species (see Cardona and Carmena, 2013; Carmena and Cardona, 2013). *E. canadensis* can be transmitted through both domestic and sylvatic life cycles, whereas *E. felidis*, *E. multilocularis*, *E. shiquicus*, *E. oligarthrus*, and *E. vogeli* are primarily circulating in wildlife cycles,

although peri-domestic or synanthropic cycles may also occur in some geographic areas (Deplazes et al., 2003; Nakao et al., 2013a). *E. granulosus* s.s. and *E. multilocularis* are the most clinically relevant species involved in human infections, causing cystic echinococcosis (CE) and alveolar echinococcosis (AE), respectively. Because *Echinococcus* species/genotypes have marked differences in host infectivity and specificity, geographical distributions, zoonotic potential, development, and pathogenicity (McManus, 2013), molecular epidemiological data are valuable not only to estimate the genotype frequencies of the parasite present in a given region, but also to ascertain its transmission dynamics.

In this review we summarize current global knowledge on the geographical and molecular diversity of *Echinococcus* spp. in wildlife definitive hosts. Despite its relevance and due to space constraints, mention to intermediate wildlife hosts has been kept to a minimum. Instead, and in line with the “One Health” thinking, we have attempted to integrate this information in the context of the available epidemiological data on *Echinococcus* infection in domestic (including dog) animal and human populations. Particular attention has been paid to the discussion of wildlife/livestock/human interfaces, including the significance of potential spill-over events between wildlife and domestic cycles, and their implications in veterinary public health. Bibliographic search was conducted in PubMed covering the period from 2000 to date and favouring publications with an English abstract. Geographical sub-regions used here followed the classification proposed by the Statistics Division of the United Nations (available at <http://unstats.un.org/unsd/methods/m49/m49regin.htm>).

2. Identifying *Echinococcus* infection in wild carnivorous species

A variety of techniques are currently available for the *post mortem* and *in vivo* detection of *Echinococcus* spp. adult worms in wild carnivore definitive hosts, either at individual or population levels. The most reliable procedures are based on parasite detection at necropsy and subsequent identification following specific morphological criteria such as the size of the gravid proglottid and the position of the genital pore. The sedimentation and counting (SCT) technique is regarded as the gold standard method (Eckert, 2003). SCT is designed to examine the whole intestinal content of the animal under study, allowing the detection of worm burdens as low as a single parasite. Therefore, the diagnostic sensitivity and specificity of SCT are close to 100% (Hofer et al., 2000). Modified versions of this method have been developed soon thereafter, including the shaking in a vessel (SVT) technique (Duscher et al., 2005) and the scraping, filtration, and counting (SFCT) technique (Geszy et al., 2013), with improved sample processing efficiencies and even diagnostic sensitivities than those reported for SCT. Also less demanding in terms of labour and time requirements, the intestinal scraping technique (IST) and its variants are better suited, and widely used, for epidemiological surveys involving large number of samples. However, because IST is based on the stereomicroscopic

examination of a limited number of intestinal thick smears, parasites in low number may be overlooked. Reported diagnostic sensitivities for IST varies from 76% to 100% depending on the reference technique considered (SCT or copro-PCR), the worm burden of the infected animals, and the experience of the staff conducting the test (Dinkel et al., 1998; Hofer et al., 2000; Tackmann et al., 2006). Necropsy-based procedures are also a source of parasitic material for downstream molecular studies and allow the estimation of worm burden, a key parameter for the mathematical modelling of *Echinococcus* transmission in a given area and the developing of control programmes. However, *post mortem* diagnosis based on morphological discrimination is only possible to some degree with well preserved and processed adult worms, an important issue in those regions where different *Echinococcus* species occur sympatrically. In addition, these methods need to meet specific safety precautions to prevent accidental exposure to infective *Echinococcus* eggs. For instance, removed intestines must be deep-frozen at -80°C for at least two days to assure the inactivation of the parasite prior to necropsy.

Intravital diagnostic tests, although usually achieving lower sensitivities and specificities compared to *post-mortem* techniques, are safer and lesser time-consuming, allow the processing of larger number of samples per time unit, and offer a considerable flexibility as they can be used with samples collected from dead or living animals or from the environment. These features made *in vivo* diagnostic techniques particularly suited for mass-screening epidemiological surveys. Detection of *Echinococcus* copro-antigens from faecal samples by ELISA (CpAg-ELISA) assays is widely used. This technique provides good diagnostic sensitivities (84–95%) with moderate to high worm burdens, although significantly lower values are expected to be obtained in definitive hosts carrying few parasites (Carmena et al., 2006, 2007; Eckert, 2003). In addition, CpAg-ELISA tests are able to detect pre-patent infection, and obtained optical density results correlate relatively well with infection intensities (Lahmar et al., 2007). Importantly, the diagnostic efficiency and field applicability of this method is largely dependent on its correct optimization and the consideration of the physical environmental (e.g. geographic area, climate, humidity) and biological (e.g. host population densities, worm burden, parasite's strain) parameters that may influence the study. Additionally, a number of PCR-based tests are also available for the specific detection of *Echinococcus* DNA directly on faeces, enriched taeniid egg preparations or the whole tapeworm (Deplazes et al., 2011; Dinkel et al., 2004). These methods are highly sensitive (89–94%), with specificities close to 100% (Eckert, 2003). However, these techniques are laborious and relatively costly, features that limit considerably its applicability in field surveys. Consequently, PCR is better suited and more frequently used as confirmatory test (particularly in animal populations where low parasite prevalences are suspected) and for genotyping purposes (Deplazes et al., 2003). Finally, immunodiagnostic assays for the detection of specific antibodies are not a feasible approach for the identification of *Echinococcus* infection in wildlife definitive hosts, except perhaps as a

validation test in captive or semi-captive animal populations.

3. Echinococcosis in African wild carnivorous species

Echinococcosis is largely known to affect all North African countries stretching from Morocco to Egypt (Dakkak, 2010). The infection is also present in North-eastern Africa, with hyper-endemic foci in areas of Ethiopia, Kenya, Sudan, Tanzania and Uganda (Wahlers et al., 2012). These regions comprise semi-arid mixed woodland, scrub and grassland traditionally exploited by nomadic or semi-nomadic pastoralists and their livestock, conditions particularly suited to the transmission of the domestic cycle of *Echinococcus*. Echinococcosis is generally assumed to be infrequent in Western, Central and Southern Africa, although assessing the actual situation of the infection in these areas is difficult because of the lack of complete, reliable, and updated epidemiological data. Overall, a high variability in the prevalence and geographic distribution of the infection in human and livestock populations has been observed in this continent (Romig et al., 2011; Wahlers et al., 2012). This phenomenon seems to be dependent on the density of susceptible intermediate hosts and also on the parasite species involved, which greatly influence host specificity and pathogenicity.

Echinococcosis in Africa can be transmitted in domestic, synanthropic or sylvatic cycles. The domestic cycle is maintained between dogs acting as definitive host and a number of livestock species as intermediate hosts (see Cardona and Carmena, 2013; Carmena and Cardona, 2013). Well-established, independent wildlife cycles are also known to exist among major wild carnivores within the families canidae (fox, jackal) and felidae (lion) and their prey (mainly ungulate) species, particularly in protected national parks and game reserves. Cape hunting dogs and hyenas seem to have a minor role as definitive host for *Echinococcus* spp. due to their low numbers and susceptibility to the infection, respectively. Wild intermediate hosts include a large variety of ungulate species, rodents, and non-human primates. High infection rates have been reported in zebras, warthogs, and buffaloes, suggesting that these species are the major contributors to the transmission of the parasite (Jenkins and Macpherson, 2003; Huttner and Romig, 2009; Romig et al., 2011). More relevant from a veterinary public health perspective is the existence of areas where domestic and sylvatic life cycles of the parasite overlap. This situation has been intensified in later years due to the rapid expansion of livestock and crop farming and the subsequent entrenchment of wildlife on conservation areas. Wherever the wildlife/livestock/human interface occurs, it should be regarded as a two-way street with the potential for the transmission of *Echinococcus* spp. in either direction: from the wild to domestic animals, or from domestic animals to wildlife (Jenkins and Macpherson, 2003; Huttner and Romig, 2009; Romig et al., 2011; Thompson, 2013).

Recent molecular epidemiological studies have confirmed the presence of *E. granulosus* s.s., *E. ortleppi*, and *E. canadensis*, circulating in African livestock species and

humans (Cardona and Carmena, 2013; Alvarez Rojas et al., 2014). No updated genotyping data are currently available from dog isolates (see Carmena and Cardona, 2013), although earlier studies have reported the presence of the G1 and G6 strains in Kenyan dogs from the Turkana district (Wachira et al., 1993). Regarding wildlife, *E. felidis* has been found infecting wild carnivores including lions and hyenas (Huttner et al., 2008; Huttner and Romig, 2009), whereas warthog is the only intermediate host species where this *Echinococcus* species has been confirmed to date (Huttner et al., 2009). Moreover, recent molecular and phylogenetic evidence has demonstrated that *E. felidis* and *E. granulosus* s.s. are sister species (Huttner et al., 2008; Nakao et al., 2013a), raising the question as whether *E. felidis* could be also infective to humans and domestic animals. This issue is relevant because previous molecular surveys in Africa were based on genotyping methods that do not discriminate between *E. granulosus* s.s. and *E. felidis*. In an attempt to clarify this situation, Huttner et al. (2009) re-examined 412 hydatid cysts from humans and livestock species from Kenya, characterizing all of them as *E. granulosus* s.s. or *E. canadensis*. Although limited, these results seem to indicate that *E. felidis* is restricted to sylvatic cycles and probably poses little zoonotic potential, although the actual extent of this hypothesis should be corroborated in future studies. Interestingly, *E. granulosus* s.s. G1 strain and *E. ortleppi* have been identified in a warthog from Uganda and a zebra from Namibia, respectively (Obwaller et al., 2004; Huttner et al., 2009). Whether these findings indicate true primary wildlife cycles of *E. granulosus* s.s. and *E. ortleppi* or an accidental spill-over event from domestic cycles of the parasite is still a matter of debate. *E. multilocularis* is apparently absent or very rare in the African continent. Three allegedly human AE cases have been reported in Morocco (Maliki et al., 2004) and Tunisia (Zitouna et al., 1985), but the infection has not been documented in wildlife or domestic dogs to date.

Recent prevalence and molecular studies on *Echinococcus* spp. infection in African wild definitive host species have been carried out only in Tunisia and Uganda (Table 1). *E. granulosus* s.s. G1 genotype has been found infecting foxes (13%), genets (75%), hyenas, and jackals (4–20%) from Tunisia, whereas *E. felidis* have been identified in hyenas (20%) and lions (72%) from Uganda. These infection rates should be interpreted with caution due to the relatively low number of samples tested in these studies. The scarcity of epidemiological and molecular data currently available clearly indicates that more research effort is needed to better elucidate the genotype frequencies, geographical distribution, host range, and pathogenicity to humans of *Echinococcus* spp. (particularly *E. felidis*) in African wildlife.

4. Echinococcosis in Asian wild carnivorous species

E. granulosus sensu lato (s.l.) is endemic or re-emerging in large parts of Asia including East and Central Asian countries (Sadjadi, 2006; Torgerson et al., 2006), North and Western China (McManus, 2010; Wang et al., 2008), and North-eastern Siberia (Rausch, 2003). Only sporadic or fragmentary epidemiological information is currently available from the Arab states bordering the

Table 1
Prevalence and molecular epidemiology of echinococcosis in African wild definitive host species (2000 onwards).

Country	Host species	No. samples ^a	Diagnostic procedure	<i>Echinococcus</i> species and prevalence (%)	Intensity of infection	Molecular characterization			Reference
						No. isolates ^c	Gene markers	Genotype frequency (%)	
Tunisia	Fox	15	Copro-PCR	<i>E.g. s.s.</i> (13.3%)	–	–	<i>EgG1 Haelll</i>	G1 (100%)	Lahmar et al. (2009)
	Fox	15	CpAg-ELISA	<i>Echinococcus</i> spp. (13.3%)	–	–	–	–	Lahmar et al. (2009)
	Genet	4	CpAg-ELISA	<i>Echinococcus</i> spp. (75.0%)	–	–	–	–	Lahmar et al. (2009)
	Hyena	1	CpAg-ELISA	<i>Echinococcus</i> spp. (100%)	–	–	–	–	Lahmar et al. (2009)
	Jackal	5	Necropsy	<i>E.g. s.s.</i> (20.0%)	72 ^b	1 (AW)	<i>rrnS</i>	G1 (100%)	Lahmar et al. (2009)
	Jackal	28	Copro-PCR	<i>E.g. s.s.</i> (17.9%)	–	–	<i>EgG1 Haelll</i>	G1 (100%)	Lahmar et al. (2009)
	Jackal	28	CpAg-ELISA	<i>Echinococcus</i> spp. (4.3%)	–	–	–	–	Lahmar et al. (2009)
Uganda	Hyena	5	Coproscopy/PCR	<i>E.f.</i> (20.0%)	–	1 (E)	<i>Nad1</i>	<i>E.f.</i> (100%)	Huttner et al. (2009)
	Lion	–	–	–	–	1 (E)	<i>cob1, cox1, ef1a, elp, nad1, rrnL, rrnS</i>	<i>E.f.</i> (100%)	Huttner et al. (2008)
	Lion	47	Coproscopy/PCR	<i>E.f.</i> (72.3%)	–	34 (E)	<i>nad1</i>	<i>E.f.</i> (100%)	Huttner et al. (2009)

cob1: mitochondrial cytochrome b; *cox1*: mitochondrial cytochrome c oxidase subunit 1; *E.f.*: *Echinococcus felidis*, *E.g. s.s.*: *Echinococcus granulosus* sensu stricto; *ef1a*: nuclear genes for elongation factor 1 alpha; *EgG1 Haelll*: *E. granulosus* repeated sequence; *elp*: ezrin-radixin-moesin (ERM)-like protein; *nad1*: mitochondrial NADH dehydrogenase subunit 1; NS: not specified; PCR: polymerase chain reaction; *rrnL*: large subunit of ribosomal RNA; *rrnS*: small subunit of ribosomal RNA.

^a Number of definitive host individuals analyzed by necropsy, or number of faecal supernatants analyzed by coproscopy, CpAg-ELISA (ELISA for the detection of *Echinococcus* copro-antigens), or Copro-PCR (PCR for the detection of *Echinococcus* copro-DNA).

^b Mean intensity of infection (mean number of adult worms per infected definitive host).

^c An isolate is defined here as parasite DNA extracted from *Echinococcus* adult worms (AW) or taeniid eggs (E) from an individual, infected animal.

Persian Gulf and the Southeast Asian countries (Schantz et al., 1995). Domestic transmission cycles of *E. granulosus* s.s., *E. canadensis*, and *E. ortleppi* are known to be circulating between dogs and a variety of livestock species in the above mentioned regions (see Cardona and Carmena, 2013). Regarding wildlife, *E. granulosus* s.l. has been found infecting wild carnivores such as foxes, jackals, and wolves in China (reviewed in Wang et al., 2008), Iran (Beiromvand et al., 2011; Dalimi et al., 2002) and Kazakhstan (Abdybekova and Torgerson, 2012), although in many of these studies species-level identification of the parasite causing the infection was not achieved (see below). In addition, *E. shiquicus*, a recently identified *Echinococcus* species in China, is also known to be transmitted between red foxes and pikas (Xiao et al., 2005). *E. multilocularis* has been recorded from Armenia, Azerbaijan, Russia, the Central Asian Republics, Mongolia, China, and North of Japan, where it is predominantly transmitted between wild carnivores (foxes, jackals, wolves and raccoon dogs) and a number of small mammal species including voles, lemmings, hares, and pikas (Vuitton et al., 2003; Wang et al., 2008). Sympatric occurrence of various *Echinococcus* species/genotypes and overlapping of domestic and sylvatic cycles of the parasite take place in certain geographical areas, as in the case of the Tibetan Plateau of China.

4.1. Echinococcosis in wild carnivorous species from northern Asia

Echinococcus spp. is endemic to the subarctic tundra and boreal taiga areas of Northern Eurasia, where the parasite is primarily transmitted in the wild (Rausch, 2003). Life cycles of *E. canadensis* G6, G8, and G10 genotypes (maintained between elk and wolves) and the North American genotype of *E. multilocularis* (maintained between voles/lemmings and foxes) are known to occur sympatrically in this region (Konyaev et al., 2013). A human CE patient has been demonstrated to be infected with *E. canadensis* G10, but no human AE cases have been reported in recent years, indicating that the North American genotype of *E. multilocularis* may pose little pathogenicity to humans (Konyaev et al., 2013). No evidence (e.g. genotyping studies in dog populations) supporting the existence of synanthropic cycles of *E. canadensis* G8–G10 or *E. multilocularis* is currently available for the region, suggesting that the rare human infections reported to date are most likely due to direct contact with wild carnivores.

4.2. Echinococcosis in wild carnivorous species from Central Asia

Published studies on the prevalence of *Echinococcus* spp. in wildlife species from this geographic area are restricted to Kazakhstan and Kyrgyzstan. Although limited, available epidemiological data demonstrate that both wolves and foxes are important definitive host species in maintaining the transmission cycle of the parasite in these countries (Table 2). In Kazakhstan, *E. granulosus* s.l. has been reported in wolves at high prevalence (19%) and abundance of infection (1275 worms per examined animal). Saiga antelopes,

roe deer, and wild boars are the most likely intermediate host species (Abdybekova and Torgerson, 2012). However, absence of molecular data from wildlife species and domestic animals makes difficult to assess the veterinary public health significance of this finding. A similar situation takes place in Kyrgyzstan, where *E. multilocularis* is a very common parasite of foxes (64% prevalence) but epidemiological information on human AE is lacking.

4.3. Echinococcosis in wild carnivorous species from West Asia

While domestic cycles of *Echinococcus* s.s. and/or *E. canadensis* have been documented in Iraq, Jordan, Lebanon, Saudi Arabia, and Turkey in recent years, the current status of *Echinococcus* infection in wildlife definitive and intermediate host species from these countries is unknown. However, sylvatic cycles of *E. granulosus* s.l. and *E. multilocularis* are likely to occur in the eastern regions of Turkey and Iraq bordering Iran, where these *Echinococcus* species are known to be endemic (see below). More field studies are necessary to confirm the extent of this hypothesis.

4.4. Echinococcosis in wild carnivorous species from South Asia

Iran is the only country from this geographical region where the presence of *Echinococcus* spp. has been consistently surveyed in natural host populations to date. Both *E. granulosus* s.l. and *E. multilocularis* have been reported infecting foxes, hyenas, jackals, and wolves at variable prevalence and abundance rates (Table 2), particularly in the North-western part of the country. However, prevalence data should be interpreted with caution in some cases due to the limited numbers of animals studied. Dual infections by *E. granulosus* s.l. and *E. multilocularis* have been found in two jackals and a single fox at necropsy, demonstrating that these *Echinococcus* species occur sympatrically in Iran (Beiromvand et al., 2011). Sylvatic cycles are assumed to be maintained through wild sheep and gazelles acting as intermediate host species (Dalimi et al., 2002). Unfortunately, the lack of genotyping data does not allow assessing the zoonotic potential of wildlife isolates in a country where the vast majority of human CE infections characterized to date are caused by *E. granulosus* s.s. and *E. canadensis* G6 (see Alvarez Rojas et al., 2014). However, spill-over events from domestic to sylvatic cycles are suspected to be frequent in areas where infected viscera from butchered livestock are known to be accessible to jackals and foxes (Dalimi et al., 2006).

Human and/or livestock CE cases have been reported from Afghanistan, India, Nepal, and Pakistan, where *E. granulosus* s.s. is the most prevailing *Echinococcus* species (reviewed in Cardona and Carmena, 2013; Alvarez Rojas et al., 2014). Although the frequency distribution and zoonotic potential of echinococcosis in wildlife species is currently unknown, available epidemiological and molecular data seems to indicate that the parasite is primarily transmitted through domestic cycles in these countries.

Table 2
Prevalence and molecular epidemiology of echinococcosis in Asian wild definitive host species (2000 onwards).

Country	Host species	No. samples ^a	Diagnostic procedure	<i>Echinococcus</i> species and prevalence (%)	Intensity of infection	Molecular characterization			Reference
						No. isolates ^d	Gene markers	Genotype frequency (%)	
China	Fox	42	Necropsy	<i>E.m.</i> (4.8%)	~1150 ^b	–	–	–	Tang et al. (2004)
	Fox	16	Necropsy	<i>Echinococcus</i> spp. (43.8%)	NS	7 (AW)	<i>cob1</i> , <i>cox1</i> , <i>elp</i> , <i>nad1</i> , <i>rrnL</i> , <i>rrnS</i> , <i>cox1</i>	<i>E.m.</i> (14.3%); <i>E.s.</i> (85.7%)	Xiao et al. (2005)
	Fox	13	Copro-PCR	<i>E.m.</i> (15.4%)	–	–	–	–	Vaniscotte et al. (2011)
	Fox	126	Copro-PCR	<i>E.s.</i> (40.5%); <i>E.m.</i> (34.9%)	–	–	–	–	Jiang et al. (2012)
Iran	Wolf	9	Necropsy	<i>E.g. s.l.</i> (33.3%)	NS	–	–	–	Tang et al. (2004)
	Fox	60	Necropsy	<i>E.g. s.l.</i> (5.0%)	12 ^b	–	–	–	Dalimi et al. (2002)
	Fox	22	Necropsy	<i>E.g. s.l.</i> (4.5%)	NS	–	–	–	Dalimi et al. (2006)
	Fox	79	CpAg-ELISA	<i>Echinococcus</i> spp. (16.7%)	–	–	–	–	Zare-Bidaki et al. (2009)
	Fox	3	Copro-PCR	<i>E.g. s.l.</i> (100%); <i>E.m.</i> (100%)	–	–	<i>nad1</i> , <i>rrnS</i>	–	Beiromvand et al. (2011)
	Hyena	1	Copro-PCR	<i>E.g. s.l.</i> (100%); <i>E.m.</i> (100%)	–	–	<i>nad1</i> , <i>rrnS</i>	–	Beiromvand et al. (2011)
	Jackal	86	Necropsy	<i>E.g. s.l.</i> (2.3%)	6.5 ^b	–	–	–	Dalimi et al. (2002)
	Jackal	10	Necropsy/IST/SCT	<i>Echinococcus</i> spp. (50.0%)	>1000	–	–	–	Beiromvand et al. (2011)
	Jackal	9	Copro-PCR	<i>E.g. s.l.</i> (66.7%); <i>E.m.</i> (100%)	–	–	<i>nad1</i> , <i>rrnS</i>	–	Beiromvand et al. (2011)
	Wolf	1	Necropsy/IST/SCT	<i>Echinococcus</i> spp. (100%)	1–100	–	–	–	Beiromvand et al. (2011)
	Wolf	1	Copro-PCR	<i>E.g. s.l.</i> (100%); <i>E.m.</i> (100%)	–	–	<i>nad1</i> , <i>rrnS</i>	–	Beiromvand et al. (2011)
	Wolf	1	Copro-PCR	<i>E.g. s.l.</i> (100%); <i>E.m.</i> (100%)	–	–	<i>nad1</i> , <i>rrnS</i>	–	Beiromvand et al. (2011)
Japan	Fox	155	CpAg-ELISA	<i>Echinococcus</i> spp. (21.3%)	–	–	–	–	Tsukada et al. (2000)
	Fox	285	CpAg-ELISA	<i>Echinococcus</i> spp. (42–60%)	–	–	–	–	Tsukada et al. (2002)
	Fox	67	Necropsy	<i>E.m.</i> (56.7%)	74,200 ^b	–	–	–	Yimam et al. (2002)
	Fox	1	Necropsy	<i>E.m.</i> (100%)	8000 ^b	–	–	–	Kamiya et al. (2003)
	Fox	139	CpAg-ELISA/Coproscopy/PCR	<i>E.m.</i> (45.5–56.5%)	–	21 (E)	<i>nad1</i> , <i>rrnS</i>	<i>E.m.</i> (100%)	Lagapa et al. (2009)
	Fox	209	CpAg-ELISA/Coproscopy/PCR	<i>E.m.</i> (34.0%)	–	27 (E)	<i>cox1</i>	<i>E.m.</i> (100%)	Nonaka et al. (2009)
	Raccoon dog	13	Necropsy	<i>E.m.</i> (23.1%)	472 ^b	–	–	–	Yimam et al. (2002)
	Wolf	41	Necropsy	<i>E.g. s.l.</i> (19.5%)	1275 ^c	–	–	–	Abdybekova and Torgerson (2012)

Table 2 (Continued)

Country	Host species	No. samples ^a	Diagnostic procedure	Echinococcus species and prevalence (%)	Intensity of infection	Molecular characterization			Reference
						No. isolates ^d	Gene markers	Genotype frequency (%)	
Kyrgyzstan	Fox	151	Necropsy/SCT	<i>E.m.</i> (63.6%)	8668 ^c	–	–	–	Ziadinov et al. (2010)
Mongolia	Fox	302	Necropsy/SCT	<i>E.m.</i> (5.0%)	NS	NS	<i>cox1</i>	<i>E.m.</i> (100%)	Ito et al. (2013)
	Wolf	118	Necropsy/SCT	<i>Echinococcus</i> s.l. (4.2%); <i>E.m.</i> (3.4%)	NS	NS	<i>cox1</i>	G6/7 (22.2%); G10 (33.3%); <i>E.m.</i> (44.5%)	Ito et al. (2013)

cox1: mitochondrial cytochrome b; *cox1*: mitochondrial cytochrome c oxidase subunit 1; *E.g.*: *Echinococcus granulosus*; *elp*: ezrin-radixin-moesin (ERM)-like protein; *E.m.*: *Echinococcus multilocularis*; *E.s.*: *Echinococcus shiquicus*; *IST*: intestinal scraping technique; *mtad1*: mitochondrial NADH dehydrogenase subunit 1; NS: not specified; PCR: polymerase chain reaction; rml: large subunit of ribosomal RNA; rms: small subunit of ribosomal RNA; SCT: sedimentation and counting technique.

^a Number of definitive host individuals analyzed by necropsy, or number of faecal supernatants analyzed by coproscopy, CpAg-ELISA (ELISA for the detection of *Echinococcus* copro-antigens), or Copro-PCR (PCR for the detection of *Echinococcus* copro-DNA).

^b Mean intensity of infection (mean number of adult worms per infected definitive host).

^c Mean abundance of infection (mean number of adult worms per definitive host examined).

^d An isolate is defined here as parasite DNA extracted from *Echinococcus* adult worms (AW) or taeniid eggs (E) from an individual, infected animal.

4.5. Echinococcosis in wild carnivorous species from East Asia

Compared to the relatively abundant amount of information on *Echinococcus* infection in human and domestic animal populations in China, epidemiological data from wildlife species is much scarcer. To date, three *Echinococcus* (*E. multilocularis*, *E. shiquicus*, and *E. granulosus* s.l.) species have been described infecting wild animals as natural hosts in China. *E. multilocularis* is transmitted through foxes and arvicoline rodents/lagomorphs (mainly voles and hares) acting as definitive and intermediate host species, respectively. Reported infection rates in foxes varied from 5% to 35% (Table 2). Landscapes favouring small mammal diversity (e.g. grasslands) and promoting population outbreaks of suitable intermediate host species have been identified as a key factor in the regulation of the transmission of *E. multilocularis* in China (Giraudoux et al., 2013). Recent phylogeographic studies on *E. multilocularis* have also revealed that Chinese isolates from different definitive and intermediate host species cluster together in what it is now known as the Asian genotype of the parasite (Nakao et al., 2009, 2010). *E. shiquicus* also uses foxes as definitive hosts (infection rate: 40%), but the larval stage of this newly described *Echinococcus* species has only been documented infecting pikas in the Tibetan Plateau (Xiao et al., 2005). Importantly, the finding that mature *E. multilocularis* and *E. shiquicus* adult worms are morphologically very similar has cast doubts on the validity of the *Echinococcus* species assigned to parasites obtained in definitive hosts from this region in previous studies (Xiao et al., 2006). In addition, the fact that pikas can harbour concurrent infections with both *E. multilocularis* and *E. shiquicus* strongly suggests that dual infections should also be expected in foxes (Xiao et al., 2006). A morphologically distinct variant of *E. multilocularis* has been identified in a fox from the region of Inner Mongolia of China (Tang et al., 2004). Although lack of molecular data impede the definitive genotype assignment of this variant, its morphometric features do not match those described for *E. shiquicus* (Xiao et al., 2005). Finally, *E. granulosus* s.l. has been found at high prevalence (33%) rates in wolves (Table 2). At present it is unclear whether *E. granulosus* s.l. infections in wolves are the product of spill-over events from domestic cycles of the parasite, or this species is actually circulating in a true sylvatic cycle. Importantly, *E. multilocularis* and *E. shiquicus* peri-domestic cycles are known to exist through dogs preying on small mammals in close proximity to human settlements in endemic areas of the country (Vaniscotte et al., 2011; Boufana et al., 2013). In China, human infections have been confirmed for all species except *E. shiquicus* (Vuitton et al., 2003; Alvarez Rojas et al., 2014). Therefore, the zoonotic potential of *E. shiquicus* remains to be elucidated.

E. multilocularis is the only *Echinococcus* species present in Japan, where the infection is endemic only in the northern island of Hokkaido. Foxes and voles are the main wildlife hosts involved in the sylvatic transmission cycle of the parasite, although raccoon dogs can also serve as definitive hosts (Yimam et al., 2002). In

addition, there is growing epidemiological evidence supporting the existence of a synanthropic cycle involving domestic dogs (reviewed in [Carmena and Cardona, 2013](#)) as a consequence of the increase in fox populations in urban and suburban areas including protected forest parks and woodlands ([Tsukada et al., 2000](#)). Reported prevalences in foxes, most of them based on CpAg-ELISA results, varied from 21% to 57% ([Table 2](#)). These figures, combined with elevated worm burdens (between 8000 and more than 74,000 adult worms per infected animal), provide a good insight into the high environmental contamination with *E. multilocularis* eggs caused by infected foxes in Japan.

Sympatric occurrence of *E. canadensis* G6–G7 and G10 genotypes have been found in wolves living in the mountainous areas of western Mongolia. Interestingly, the G6–G10 complex is also the most frequently identified in human CE cases from this part of the country ([Jabbar et al., 2011](#)). In addition, wolves and foxes can also harbour infections by the Mongolian (and presumably by the Asian) genotype of *E. multilocularis*. This intraspecific variant is responsible for two of the three human AE cases characterized to date in Mongolia, the remaining one being infected with the Asian genotype of the parasite ([Ito et al., 2010](#)). Taking together, these data seem to suggest that, in Mongolia, human CE (by *E. canadensis*) and AE cases are most likely caused by direct contact with wild canids, whereas human infections by *E. granulosus* s.s. would be primarily acquired through domestic cycles involving dogs.

4.6. Echinococcosis in wild carnivorous species from Southeast Asia

Based on incidental human CE data, *Echinococcus* infection seems rare in Southeast Asian countries, where only sporadic cases have been documented in Indonesia, Malaysia, Singapore, and Thailand in the last decades ([Wiwanitki, 2004](#)). Human CE is unreported from Cambodia, Lao People's Democratic Republic, and Myanmar. Whether the parasite is maintained through sylvatic life cycles or absent in these countries is currently unknown. More research should be conducted to clarify this issue.

5. Echinococcosis in European wild carnivorous species

Historically, endemic regions for *E. multilocularis* in Europe were restricted to a core area comprising East-Central France, Switzerland, Southern Germany, and Western Austria ([Romig et al., 2006a](#)). However, the marked increasing of fox populations initiated during the 1990s as a result of successful campaigns of oral vaccination against rabies has led to a geographical spread of the parasite northwards within Belgium and the Netherlands, and also towards South-eastern areas including Central Germany, Slovakia, Hungary, and Romania ([Vervaeke et al., 2006](#); [Davidson et al., 2012](#)). This relatively recent expansion is supported by analysis on frequency and distribution of microsatellite genotypes consistent with

a “mainland-island” transmission model where ancestral foci spread to peripheral regions by fox mobility and migration ([Knapp et al., 2008, 2012](#); [Casulli et al., 2010](#)). Consequently, reports of first findings of the parasite have been documented in Denmark in 2006 ([Saeed et al., 2006](#)), in Estonia in 2005 ([Moks et al., 2005](#)), in Italy in 2002 ([Manfredi et al., 2002](#)), and in Sweden in 2011 ([Osterman Lind et al., 2011](#)). Nonetheless, whether this spread of *E. multilocularis* represents stable endemic areas previously unnoticed due to lack of surveillance efforts or inaccurate diagnostic tools, or whether the parasite has truly expanded its range recently remains unclear in some cases.

In Europe, *E. multilocularis* is transmitted in a predominantly sylvatic cycle involving primary foxes and secondary jackals, raccoon dogs, and wolves as definitive hosts and a large number of species of microtine or arvicolid rodents as intermediate hosts ([Vuitton et al., 2003](#); [Romig et al., 2006b](#)). As in the case of China (see [Giraudoux et al., 2013](#)), transmission of *E. multilocularis* is more frequently enhanced in areas dominated by grassland or agriculturally altered landscapes that favour the development of high population densities of small rodents ([Romig et al., 2006b](#)). Environmental variables including annual temperature and rainfall rates and soil humidity levels have also been identified as relevant factors that influence the distribution pattern of the parasite ([Miterpakova et al., 2006](#)). Linked to the increase in fox populations, an inevitable expansion to urban areas has been documented in recent years. Therefore, the presence of *E. multilocularis* has been confirmed in foxes roaming in Budapest ([Casulli et al., 2010](#)), Copenhagen ([Kapel and Saeed, 2000](#)), Geneva ([Fischer et al., 2005](#); [Reperant et al., 2007](#)), Nancy ([Robardet et al., 2008](#)), Paris ([Combes et al., 2012](#)), Prague ([Martinek et al., 2001b](#)), and Zürich ([Hofer et al., 2000](#)). This situation may enable the establishment of synanthropic cycles of the parasite maintained among infected small rodents and domestic dogs that occasionally prey on them ([Deplazes et al., 2004](#); [Reperant et al., 2007](#); [Robardet et al., 2008](#)), increasing the risk of AE transmission to humans.

Compared to *E. multilocularis*, epidemiological data on the frequency and distribution of *E. granulosus* s.l. in European wildlife is scarce. Sylvatic cycles of the parasite have been partially documented in a limited number of countries, mainly in North (Estonia, Latvia, and Finland) and South (Italy, Portugal and Spain) Europe ([Hirvelä-Koski et al., 2003](#); [Guberti et al., 2004](#)). Whatever the case may be, the wolf is the only wild carnivorous species identified as definitive host of *E. granulosus* s.l. to date.

5.1. Echinococcosis in wild carnivorous species from northern Europe

Both Great Britain and Ireland are considered *E. multilocularis*-free areas, as the presence of the parasite could not be demonstrated in large field studies with wild fox populations ([Learnmount et al., 2012](#); [Murphy et al., 2012](#)). A captive beaver imported from Germany was found infected with *E. multilocularis* metacestodes in Great Britain in 2011 ([Barlow et al., 2011](#)). Although the risk of accidental introduction and further dispersal of the

disease through imported beavers was judged low, this incident highlights the usefulness of surveillance schemes in detecting events potentially relevant to veterinary public health. CE is re-emerging in certain areas of Wales (Mastin et al., 2011), where domestic cycles of *E. granulosus* s.s. and *E. equinus* are known occur. At present, the relative impact of this situation to human health is unclear, although the reported incidence of human CE in this area is very sporadic (Alvarez Rojas et al., 2014). *E. granulosus* s.l. does not seem to be circulating in the wild in these countries.

In Denmark, the first record of *E. multilocularis* in wild foxes was published in 2006 (Saeed et al., 2006). Infected dogs returning from endemic areas were initially thought as the most likely explanation for the accidental introduction of the infection in the country. As a consequence of the public health concern raised by this finding, a national surveillance programme was launched in 2011. New epidemiological data revealed a global prevalence rate of 0.7% in the Danish fox population, although a prevalence of 31% were recorded in an endemic focus in Southern Jutland near the German border (Enemark et al., 2013). Intriguingly, sub-genotyping data of one of the isolates obtained did not cluster closely with any other of the European isolates considered in the phylogenetic analysis, casting doubts about its actual origin. So far the parasite has not been detected in wolves, raccoon dogs, and badgers, and there is no information on any autochthonous human AE cases.

In Estonia, *E. multilocularis* has been identified at a prevalence of 29% in a limited number of foxes (Moks et al., 2005). In addition, there is also a sylvatic life-cycle of *E. canadensis* G10 with wolves as primary definitive hosts (Table 3) and moose as the presumably intermediate host species. Although *E. granulosus* infections in pigs have been recorded in earlier national surveys, the current status of human and animal CE in the country is unknown.

E. multilocularis has also been documented in adjacent Latvia, where the parasite has been detected in foxes, racoon dogs, and wolves at prevalence rates in the range of 6–36% (Table 3). Wolves can also harbour infections by *E. granulosus* s.l. Molecular analyses have only being performed on *E. multilocularis* isolates from foxes, revealing that the genotypes characterized belonged to the European variant of the parasite (Bagrade et al., 2008). In this country 15 cases of human CE and 29 cases of human AE have been confirmed during the period 1996–2010. The fact that the number of cases reported significantly arose from 2001 onwards seems to suggest that CE and AE are re-emerging in the country (Keiss et al., 2007; Tulin et al., 2012). Unfortunately, no epidemiological information is currently available on CE in livestock or canine echinococcosis in Latvia.

In Lithuania, *E. multilocularis* is the only *Echinococcus* species circulating in the wild reported to date. Foxes and racoon dogs are highly suitable definitive hosts (Table 3), whereas in addition to voles, muskrats can also act as intermediate host species (Mažeika et al., 2003). Strong evidence of the existence of a synanthropic cycle of the parasite comes from the finding that domestic dogs can harbour *E. multilocularis* adult worms (Bružinskaitė et al., 2009). In addition, 80 human AE cases have been diagnosed in

the country during the period 1997–2006, with most cases being registered between 2002 and 2006 (Bružinskaitė et al., 2007). As in the case of Latvia, this situation may be indicative of a re-emergence of the disease, although more research is needed to confirm the extent of this hypothesis. A domestic cycle of *E. canadensis* G6–G7 is also known to be maintained between pigs and dogs (Bružinskaitė et al., 2009) and at least seven human CE cases of unknown genotype were officially reported in the country in 2011 (EFSA, 2013). The occurrence of this *Echinococcus* species in wildlife species in Lithuania has yet to be surveyed.

Regarding the Scandinavian Peninsula, *E. multilocularis* has been identified in native foxes from Norway and Sweden at variable prevalence rates (Table 3). No records of this *Echinococcus* species are currently available from Finland. In Norway, *E. multilocularis* is restricted to the Svalbard archipelago in the Arctic Ocean, where accidental introduction of susceptible intermediate hosts (sibling voles) enabled the establishment of a sylvatic cycle of the parasite (Fuglei et al., 2008; Stien et al., 2010). Field surveys aiming to demonstrate the presence of *E. multilocularis* in shot foxes in mainland Norway have been unsuccessful (Davidson et al., 2009). In Sweden, *E. multilocularis* was first detected in the Southwest area of the country in a shot fox (Osterman Lind et al., 2011). Travelling dogs not complying with legal requirements regarding deworming procedures when entering the country were suspected as the most probable source of the parasite being introduced into the country. A subsequent epidemiological field study at national scale has shown that *E. multilocularis* is now endemic at low prevalence (0.3%) in Sweden (Wahlström et al., 2012). No records of any other *Echinococcus* species causing infection in domestic animals have been published to date in this country, although 19 CE/AE (not specified) human infections were reported in 2011 (EFSA, 2013). Finally, *E. granulosus* s.l. occurs in Eastern Finland in a sylvatic cycle between wolves and reindeer (and probably also elk). High prevalence (up to 27%) and intensity of infection (479 worms per infected animal) rates have been documented in Finnish wolves (Hirvelä-Koski et al., 2003). This *Echinococcus* species does not seem to be transmitted through domestic cycles, and only a single human CE/AE (not specified) case have been reported recently in the country (EFSA, 2013). *E. multilocularis* has never been found in Finland to date.

5.2. Echinococcosis in wild carnivorous species from western Europe

E. multilocularis is the only *Echinococcus* species circulating in the wild in western Europe, where *E. granulosus* s.l. is practically absent and restricted to marginal domestic transmission cycles (see Cardona and Carmena, 2013). A wealth of information regarding the relative frequency, geographic distribution and genetic variability of *E. multilocularis* is currently available from this geographic region (Table 3). Foxes act as the almost exclusive definitive host species, although racoon dogs can also successfully harbour the adult stage of the parasite in certain areas (e.g. Germany and Slovakia).

Table 3
Prevalence and molecular epidemiology of echinococcosis in European wild definitive host species (2000 onwards).

Country	Host species	No. samples ^a	Diagnostic procedure	<i>Echinococcus</i> species and prevalence (%)	Intensity of infection	Molecular characterization			Reference
						No. isolates ^d	Gene markers	Genotype frequency (%)	
Austria	Fox	5600	Necropsy/IST/SVT	<i>E.m.</i> (2.4%)	NS	–	–	–	Duscher et al. (2006)
Belarus	Fox	94	Necropsy	<i>E.m.</i> (7.4%)	1–5000	–	–	–	Shimalov and Shimalov (2003)
	Wolf	52	Necropsy	<i>E.g. s.l.</i> (11.5%)	1–3	–	–	–	Shimalov and Shimalov (2000)
Belgium	Fox	709	Necropsy	<i>E.m.</i> (20.2%)	NS	–	–	–	Losson et al. (2003)
	Fox	237	Necropsy/IST	<i>E.m.</i> (1.7%)	~500 ^b	–	–	–	Vervaeke et al. (2003)
	Fox	990	Necropsy	<i>E.m.</i> (24.6%)	NS	–	–	–	Hanosset et al. (2008)
Bulgaria	Jackal	–	–	–	–	3 (AW)	<i>act2, AgB-1, hbx2, nad1</i>	G1 (100%)	Breyer et al. (2004)
	Wolf	–	–	–	–	1 (AW)	<i>act2, AgB-1, hbx2, nad1</i>	G1 (100%)	Breyer et al. (2004)
Czech Republic	Fox	50	Necropsy/IST	<i>E.m.</i> (60.0%)	1–5000	–	–	–	Martinek et al. (2001b)
Denmark	Fox	782	Necropsy/IST/SCT	<i>E.m.</i> (0.3%)	18.7 ^b	NS	<i>rrnS</i>	<i>E.m.</i> (100%)	Saeed et al. (2006)
	Fox	546	Necropsy/SCT/PCR	<i>E.m.</i> (0.7%)	14 ^b	1 (AW)	<i>rrnS</i>	<i>E.m.</i> (100%)	Enemark et al. (2013)
Estonia	Fox	17	Necropsy/SCT/PCR	<i>E.m.</i> (29.4%)	227 ^b	NS	<i>nad1</i>	<i>E.m.</i> (100%)	Moks et al. (2005)
	Wolf	26	Necropsy/PCR	<i>E.g. s.l.</i> (4.3%)	41 ^b	1 (AW)	<i>nad1</i>	G10 (100%)	Moks et al. (2006)
Finland	Wolf	23	Necropsy/SCT	<i>E.g. s.l.</i> (26.1%)	479 ^b	–	–	–	Hirvelä-Koski et al. (2003)
	Wolf	362	CpAg-ELISA	<i>E.g. s.l.</i> (27.3%)	–	–	–	–	Hirvelä-Koski et al. (2003)
France	Fox	222	Necropsy/SCT	<i>E.m.</i> (19.4–63.3%)	NS	–	–	–	Raoul et al. (2001)
	Fox	149	Necropsy/SCT	<i>E.m.</i> (53.0%)	2–73,380	–	–	–	Guislain et al. (2008)
	Fox	127	Necropsy/SCT	<i>E.m.</i> (30.0%)	190 ^b	–	–	–	Robardet et al. (2008)
	Fox	358	Necropsy/SCT	<i>E.m.</i> (32.7%)	NS	–	–	–	Umhang et al. (2011)
	Fox	3307	Necropsy/SCT	<i>E.m.</i> (17.0%)	NS	–	–	–	Combes et al. (2012)
Germany	Fox	3797	Necropsy/IST	<i>E.m.</i> (2.4%)	NS	–	–	–	Staubach et al. (2001)
	Fox	4375	Necropsy/IST	<i>E.m.</i> (3.4–36.6%)	NS	–	–	–	Tackmann et al. (2001)
	Fox	268	Necropsy/IST	<i>E.m.</i> (31.0–56.0%)	NS	–	–	–	König et al., 2005
	Fox	8459	Necropsy/IST	<i>E.m.</i> (5.8–16.9%)	NS	–	–	–	Berke et al. (2008)
	Fox	2757	Necropsy	<i>E.m.</i> (17.4%)	NS	–	–	–	Denzin et al. (2009)
	Fox	181	Necropsy/IST	<i>E.m.</i> (15.0–80.0%)	20–49 ^b	–	–	–	König and Romig (2010)
	Fox	26,220	Necropsy/IST	<i>E.m.</i> (11.9–42.0%) ^e	NS	–	–	–	Staubach et al. (2011)
	Fox	NS	Necropsy/IST	<i>E.m.</i> (13.6–23.4%)	NS	–	–	–	Denzin et al. (in press)
	Raccoon dog	74	Necropsy	<i>E.m.</i> (2.7%)	NS	–	–	–	Thiess et al. (2001)
	Raccoon dog	1252	Necropsy/IST	<i>E.m.</i> (6.3–12.0%) ^e	NS	–	–	–	Schwarz et al. (2011)
Hungary	Fox	100	Necropsy/SCT	<i>E.m.</i> (5.0%)	54 ^b	5 (AW)	<i>rrnS</i>	<i>E.m.</i> (100%)	Sréter et al. (2003)
	Fox	150	Necropsy/SCT	<i>E.m.</i> (12.7%)	484 ^b	–	–	–	Sréter et al. (2004)
	Fox	840	Necropsy/SCT	<i>E.m.</i> (10.7%)	92 ^c	81 (AW)	<i>EmsB</i>	<i>E.m.</i> (100%)	Casulli et al. (2010)
	Fox	1612	Necropsy/SCT	<i>E.m.</i> (7.9–10.7%)	243–746 ^b	NS (AW)	<i>rrnS</i>	<i>E.m.</i> (100%)	Tolnai et al. (2013)
	Jackal	11	Necropsy/SCT	<i>E.m.</i> (9.1%)	412	1 (AW)	<i>rrnS</i>	<i>E.m.</i> (100%)	Széll et al. (2013)
Italy	Fox	500	Copro-PCR	<i>E.m.</i> (4.8%)	–	–	<i>rrnS</i>	–	Casulli et al. (2005)
	Wolf	119	Necropsy	<i>E.g. s.l.</i> (15.1%)	697 ^b	–	–	–	Guberti et al. (2004)

Table 3 (Continued)

Country	Host species	No. samples ^a	Diagnostic procedure	<i>Echinococcus</i> species and prevalence (%)	Intensity of infection	Molecular characterization			Reference
						No. isolates ^d	Gene markers	Genotype frequency (%)	
Latvia	Fox	45	Necropsy	<i>E.m.</i> (35.6%)	86 ^b	4 (AW)	<i>act2, atp6, cox1, nad1, rrnS</i>	<i>E.m.</i> (100%)	Bagrade et al. (2008)
	Raccoon dog	57	Necropsy	<i>E.m.</i> (21.1%)	NS	–	–	–	Bagrade et al. (2008)
	Wolf	34	Necropsy	<i>E.g. s.l.</i> (2.9%); <i>E.m.</i> (5.9%)	13–29 ^b	–	–	–	Bagrade et al. (2009)
Lithuania	Fox	206	Necropsy	<i>E.m.</i> (57.3%)	56 ^b	–	–	–	Bružinskaitė et al. (2007)
	Fox	269	Necropsy/SCT	<i>E.m.</i> (58.7%)	526 ^c	–	–	–	Bružinskaitė-Schmidhalter et al. (2012)
	Raccoon dog	85	Necropsy/SCT	<i>E.m.</i> (8.2%)	41 ^c	–	–	–	Bružinskaitė-Schmidhalter et al. (2012)
Netherlands	Fox	NS	Necropsy	<i>E.m.</i> (9.4%)	NS	–	–	–	van der Giessen and Borgsteede (2002)
	Fox	106	Necropsy/SBH	<i>E.m.</i> (9.4%)	~32 ^b	4 (E, MT)	<i>rrnS, U1snRNA</i>	<i>E.m.</i> (100%)	van der Giessen et al. (2004)
	Fox	235	Necropsy	<i>E.m.</i> (2.6–7.7%)	144 ^b	–	–	–	Takumi et al. (2008)
Norway	Fox	235	Copro-PCR	<i>E.m.</i> (5.1–11.7%)	–	–	<i>rrnS, U1snRNA</i>	–	Takumi et al. (2008)
	Fox	473	CpAg-ELISA	<i>E.m.</i> (5.0–41.0%)	–	–	–	–	Fuglei et al. (2008)
	Fox	353	Necropsy	<i>E.m.</i> (8.5%)	NS	–	–	–	Stien et al. (2010)
Poland	Fox	208	Necropsy/SCT	<i>E.m.</i> (29.8%)	NS	–	–	–	Machnicka et al. (2003)
	Fox	208	CpAg-ELISA	<i>Echinococcus</i> spp. (37.55%)	–	–	–	–	Machnicka et al. (2003)
	Fox	392	Necropsy/IST	<i>E.m.</i> (45.7%)	322 ^b	–	–	–	Dubinsky et al. (2006)
Poland	Fox	65	Necropsy/SCT	<i>E.m.</i> (6.2%)	NS	–	–	–	Reiterová et al. (2006)
	Fox	65	CpAg-ELISA	<i>Echinococcus</i> spp. (13.8%)	–	–	–	–	Reiterová et al. (2006)
	Fox	214	Necropsy/IST	<i>E.m.</i> (20.1%)	NS	–	–	–	Borecka et al. (2008)
Poland	Fox	1514	Necropsy/IST	<i>E.m.</i> (23.8%)	NS	–	–	–	Malczewski et al. (2008)
	Fox	1546	Necropsy/SCT	<i>E.m.</i> (16.5%)	2807 ^b	–	–	–	Karamon et al. (2014)
	Raccoon dog	25	Necropsy/SCT	<i>E.m.</i> (8.0%)	NS	–	–	–	Machnicka et al. (2003)
Poland	Raccoon dog	25	CpAg-ELISA	<i>Echinococcus</i> spp. (8.0%)	NS	–	–	–	Machnicka et al. (2003)
	Raccoon dog	78	Necropsy	<i>E.m.</i> (5.1%)	NS	–	–	–	Gawor and Malczewski (2005)
Portugal	Wolf	68	Coproscoy/PCR	<i>E.g. s.l.</i> (1.5%)	–	1 (E)	<i>rrnS</i>	G7 (1.5%)	Guerra et al. (2013)
Romania	Fox	28	CpAg-ELISA	<i>Echinococcus</i> spp. (17.9%)	–	–	–	–	Seres and Cozma (2008)
Russia	Fox	561	Necropsy/IST/SCT	<i>E.m.</i> (4.8%)	NS	3 (AW)	<i>nad1; rrnS</i>	<i>E.m.</i> (100%)	Siko et al. (2011)
	Fox	–	–	–	–	4 (AW)	<i>cox1</i>	<i>E.m.</i> (100%)	Konyaev et al. (2013)
	Wolf	–	–	–	–	1 (AW)	<i>cox1</i>	<i>E.m.</i> (100%)	Konyaev et al. (2013)
Russia	Wolf	–	–	–	–	4 (AW)	<i>cox1</i>	G6 (50.0%); G8 (25.0%); G10 (25.0%)	Nakao et al. (2013b)

Table 3 (Continued)

Country	Host species	No. samples ^a	Diagnostic procedure	<i>Echinococcus</i> species and prevalence (%)	Intensity of infection	Molecular characterization			Reference
						No. isolates ^d	Gene markers	Genotype frequency (%)	
Slovakia	Fox	358	Necropsy	<i>E.m.</i> (35.0%)	878 ^b	–	–	–	Dubinsky et al. (2006)
	Fox	302	Necropsy/IST/SCT	<i>E.m.</i> (10.6%)	155 ^b	–	–	–	Letková and Lazar (2006)
	Fox	2226	Necropsy/SCT	<i>E.m.</i> (31.8%)	1076 ^b	–	–	–	Miterpakova et al. (2006)
	Fox	870	CpAg-ELISA	<i>Echinococcus</i> spp. (23.2%)	–	–	–	–	Miterpakova et al. (2006)
	Fox	1328	Necropsy/SCT	<i>E.m.</i> (35.6%)	1303 ^b	–	–	–	Reiterová et al. (2005)
	Fox	745	CpAg-ELISA	<i>Echinococcus</i> spp. (21.3%)	–	–	–	–	Reiterová et al. (2005)
	Fox	152	Necropsy/SCT	<i>E.m.</i> (38.8%)	1–15,000 ^b	–	–	–	Reiterová et al. (2006)
	Fox	152	CpAg-ELISA	<i>Echinococcus</i> spp. (36.2%)	–	–	–	–	Reiterová et al. (2006)
	Fox	328	Necropsy/SCT	<i>E.m.</i> (42.7%)	9759 ^b	–	–	–	Hurníková et al. (2009)
	Raccoon dog	2	Necropsy/SCT	<i>E.m.</i> (50.0%)	NS	–	–	–	Hurníková et al. (2009)
Slovenia	Wolf	31	Copro-PCR	<i>E.m.</i> (9.7%)	–	–	rrnS	–	Martinek et al. (2001a)
	Fox	428	Necropsy/SCT	<i>E.m.</i> (2.6%)	2–> 1000	–	–	–	Rataj et al. (2010)
Spain	Wolf	27	Necropsy/IST	<i>E.g.</i> s.l. (14.8%)	71 ^b	1 (AW)	<i>cox1</i>	G1 (100%)	Sobrinho et al. (2006)
Sweden	Fox	2985	Necropsy/SCT	<i>E.m.</i> (0.1%)	NS	–	–	–	Wahlström et al. (2012)
Switzerland	Fox	388	Necropsy/SCT/IST	<i>E.m.</i> (44.3%)	108 ^b	–	–	–	Hofer et al. (2000)
	Fox	604	CpAg-ELISA	<i>Echinococcus</i> spp. (25.8%)	–	–	–	–	Stieger et al. (2002)
	Fox	523	CpAg-ELISA	<i>Echinococcus</i> spp. (25.4–47.1%)	–	–	–	–	Hegglin et al. (2003)
	Fox	267	Necropsy/SCT	<i>E.m.</i> (31.0–52.0%)	Up to 120,000	–	–	–	Fischer et al. (2005)
	Fox	35	CpAg-ELISA	<i>Echinococcus</i> spp. (20.0%)	–	–	–	–	Rehmann et al. (2005)
	Fox	543	Necropsy/SCT	<i>E.m.</i> (6.4%)	NS	–	–	–	Tanner et al. (2006)
	Fox	228	Necropsy/SCT	<i>E.m.</i> (46.3%)	NS	–	–	–	Reperant et al. (2007)
Ukraine	Fox	164	Necropsy/IST	<i>E.m.</i> (2.4%)	207 ^b	–	–	–	Kharchenko et al. (2008)

act2: nuclear *Egact2*; AgB-1: nuclear *E. granulosus* B-1 antigen; atp6: mitochondrial ATPase sub-unit 6; *cox1*: mitochondrial cytochrome c oxidase subunit 1; *E.g.*: *Echinococcus granulosus*; *E.m.*: *Echinococcus multilocularis*; EmsB: *Echinococcus multilocularis* repeated microsatellite target; *hbx2*: mitochondrial homeodomain protein 2; IST: intestinal scraping technique; *nad1*: mitochondrial NADH dehydrogenase subunit 1; NS: not specified; PCR: polymerase chain reaction; rrnS: small subunit of ribosomal RNA; *U1snRNA*: U1 spliceosomal RNA; SBH: southern blot hybridization; SCT: sedimentation and counting technique; SVT: shaking in vessel technique.

^a Number of definitive host individuals analyzed by necropsy, or number of faecal supernatants analyzed by coproscopy, CpAg-ELISA (ELISA for the detection of *Echinococcus* copro-antigens), or Copro-PCR (PCR for the detection of *Echinococcus* copro-DNA).

^b Mean intensity of infection (mean number of adult worms per infected definitive host).

^c Mean abundance of infection (mean number of adult worms per definitive host examined).

^d An isolate is defined here as parasite DNA extracted from *Echinococcus* adult worms (AW), taeniid eggs (E), or mucosal tissue (MT) from an individual, infected animal.

^e Prevalence adjusted for the sensitivity and specificity of the diagnostic technique used.

In Austria, the national prevalence of *E. multilocularis* in foxes has been reported at 2.4% for the period 1991–2004, with higher rates and emerging foci of infection in the Western and Northern parts of the country (Duscher et al., 2006). In Belgium, documented infection rates of *E. multilocularis* in foxes were in the range of 2–25%, with a noticeable gradient decreasing from East to West together with declining altitude (Losson et al., 2003). Recent epidemiological surveys suggest that, following the increase of the fox population density and distribution in recent years, the parasite has spread from previously endemic areas in middle and southern parts of the country towards the north (Vervaeke et al., 2003). In addition, muskrats have been shown to play a role as intermediate host species in the sylvatic life cycle of *E. multilocularis* (Hanosset et al., 2008). Sporadic cases of human AE and CE are known to occur in Austria and Belgium (EFSA, 2013), but the current status of canine echinococcosis in these countries is unknown. Therefore, whether human AE infections are acquired through direct contact with infected foxes or domestic dogs remains unclear.

E. multilocularis is hyper-endemic in the North-Eastern (Ardennes, Franche-Comte, Lorraine) and Massif Central regions of France, where the parasite has been consistently found at high prevalence rates (range: 17–63%) in foxes (Table 3). In line with the changes in fox population dynamics observed in other European areas, a recent large-scale epidemiological study seems to indicate that the infection is expanding westwards (Combes et al., 2012). Interestingly, over-dispersed patterns of *E. multilocularis* adult worms have been identified in different fox populations, with only a small proportion (8–12%) of the infected animals harbouring most (72–76%) of the parasitic biomass (Raoul et al., 2001; Guislain et al., 2008). This finding, together with other ecological and biological factors such as the composition and structure of the landscape and the availability of susceptible intermediate host populations, may greatly influence the transmission of *E. multilocularis* at local scale, helping to explain the heterogeneous distribution frequently observed in field surveys (Guislain et al., 2008). In addition, *E. multilocularis* urban cycles have been documented in the conurbations of Nancy (Robardet et al., 2008) and Paris (Combes et al., 2012). Importantly, the demonstration of stable populations of infected intermediate host species in wasteland areas within urban settings (Robardet et al., 2011) provides the basis for the establishment of a synanthropic transmission cycle of *E. multilocularis* maintained through domestic dogs occasionally preying on infected small mammals. In this regard, it is worth noticing that 45 new AE human cases were registered in France only in 2011, accounting for almost half (48%) of the total confirmed cases reported in the European Union in that year (EFSA, 2013). Living in AE-endemic areas, having an agricultural occupation, and having dogs were factors identified with higher risk for human AE in France (Piarroux et al., 2013). Canine echinococcosis by *E. multilocularis* has been previously reported in French farm dogs (Magnaval et al., 2004), but has yet to be reported in urban dogs.

In Germany, the geographical distribution of *E. multilocularis* in the fox population was initially thought to

be restricted to the South-western (Baden-Württemberg, Bavaria, Rhineland-Palatinate, Thuringia, and Lower Saxony) part of the country (Romig et al., 2006a). However, more recent epidemiological surveys have confirmed the spread of the parasite Northwards (Berke et al., 2008) and Eastwards (Staubach et al., 2011; Denzin et al., in press), where local foci of infection are typically found at low endemicity levels. Thus, depending on the region of origin, reported *E. multilocularis* infection rates in foxes and racoon dogs varied from 2 to 80% and 3 to 12%, respectively (Table 3). Bavarian beavers have been shown as a new suitable intermediate host species in Europe (Barlow et al., 2011). The fact that the overall prevalence of canine echinococcosis by *E. multilocularis* in Germany has been estimated at 0.2% (Dyachenko et al., 2008) provides evidence of the existence of a synanthropic cycle of the parasite. It is therefore not entirely surprising that 32 confirmed cases of human AE were notified in Germany in 2011 (EFSA, 2013), with most of them coming from endemic areas in the South-west of the country (Tackmann et al., 2001).

Switzerland constitutes, together with France and Germany, the core endemic area for *E. multilocularis* in Europe. Accordingly, high prevalence rates (20–47%) of the parasite have been consistently reported in Swiss fox populations (Table 3). In line with previously published data, a high variation in worm burdens has been frequently found in infected foxes. Sub-adult individuals have been shown to carry the major part of the parasite's biomass and, therefore, to play a major role in the spreading of the infection (Hofer et al., 2000). An *E. multilocularis* urban transmission cycle has been proven in the city of Zurich, suggesting that synanthropic cycles including rodent-catching domestic carnivores may be also possible (Hofer et al., 2000). This indeed seems to be the actual case, as infections with *E. multilocularis* adult worms have been documented both in domestic (0.4–1%) and feral (7%) dogs in the country (see Carmena and Cardona, 2013). Furthermore, the epidemiological situation of human AE in Switzerland has also experienced substantial changes in recent years: annual incidence of human AE per 100,000 population has experienced a slow but steady decline from 0.12 to 0.10 during the period 1956–2000. This trend was dramatically reversed during the period 2001–2005, for which the incidence rate raised more than twofold up to a mean of 0.26 (Schweiger et al., 2007). Taking together, all the above mentioned information strongly suggests that the increase of the incidence of human AE in Switzerland is linked to the increase in the number and proportion of infected urban foxes (Schweiger et al., 2007).

In the Netherlands, *E. multilocularis* infection in foxes has been documented at prevalence rates ranging from 5% to 12% in field epidemiological studies carried out in the provinces of Groningen and Limburg (Table 3). It is thought that the presence of the parasite in these areas is a relatively recent event linked to the global expansion of the fox population in Europe (Takumi et al., 2008). There is evidence of an infection gradient with increasing levels in north-eastern direction, towards the border with Germany (van der Giessen et al., 2004). As in the case of neighbouring Belgium, muskrats have been

identified as a susceptible intermediate host, although the role of this species in the sylvatic transmission cycle of the parasite seems minor (van der Giessen and Borgsteede, 2002). No consistent epidemiological data supporting the existence of synanthropic transmission cycles of the parasite are currently available, although two human AE cases were confirmed in the Netherlands in 2011 (EFSA, 2013).

5.3. Echinococcosis in wild carnivorous species from eastern Europe

Two *Echinococcus* species are known to be circulating in the wild in Belarus, including *E. multilocularis* in foxes and *E. granulosus* s.l. in wolves (Table 3). The current situation of human CE/AE and canine echinococcosis in the country is unknown. More research is needed to elucidate the potential impact that the presence of these parasites in wildlife species represents to humans and domestic animals.

In Bulgaria, *E. granulosus* s.s. G1 genotype has been identified in three isolates obtained from jackals and a single isolate from a wolf (Breyer et al., 2004), but the prevalence rate of the parasite in these carnivorous definitive host populations is unknown. The combined facts that *E. granulosus* s.s. G1 is responsible for all the *Echinococcus* infections genotyped in livestock species to date (see Cardona and Carmena, 2013) and that only human infections caused by *E. granulosus* s.l. ($n = 307$) have been reported in this country in 2011 (EFSA, 2013) seem to suggest that the presence of the parasite in jackals/wolves is better explained by a spill-over event from domestic cycles. Records of *E. multilocularis* in human or animal populations have yet to be published in Bulgaria.

As in other countries of Central and Easter Europe, high infection rates (60%) of *E. multilocularis* have been documented in foxes from the Klatovy district of the Czech Republic (Table 3). Aggregated patterns of worm burdens were observed, with only 13% of infected foxes carrying heavy (>1000 worms) parasite loads (Martinek et al., 2001b). Importantly, *E. multilocularis* has been also found infecting domestic dogs in a number of surveys (see Carmena and Cardona, 2013), suggesting the presence of well-established peri-urban transmission cycles of the parasite. The current status of human AE in the Czech Republic remains unknown.

In Hungary, *E. multilocularis* is the only *Echinococcus* species known to infect wildlife definitive host species. Prevalence rates of 5–13% and 9% have been reported in fox and jackal populations, respectively (Table 3). The introduction of the parasite to the country is believed to be via migrating foxes coming from highly endemic areas of neighbouring Austria and Slovakia. As a consequence, *E. multilocularis* has been now detected in foxes from 16 of the 19 Hungarian counties and even in the suburban areas of the capital, Budapest (Casulli et al., 2010). Again, the distribution of the parasite was highly over-dispersed, with only 5% of the infected foxes harbouring 93% of the total number of adult worms. This pattern was particularly accentuated in low endemic regions of the country (Casulli et al., 2010). Genetic diversity studies based on analysis of microsatellites have evidenced that all the *E. multilocularis* isolates

considered belong to the European genotype and show little genetic drift, supporting a founder effect where all the variants of the parasite circulating in Hungary constitute a peripheral subpopulation originated from a single European focus (Casulli et al., 2010). Domestic transmission cycles of *E. granulosus* s.s. and *E. canadensis* G7 are known to be present in the country (see Cardona and Carmena, 2013), and a single human CE case has been characterized as being infected with the latter genotype (Schneider et al., 2010). Human AE cases have yet to be confirmed, but it is expected that the disease will emerge in the near future.

E. multilocularis is also endemic in Poland, where the parasite has been found infecting foxes and raccoon dogs at prevalence rates in the range of 6–46% and 5–8%, respectively (Table 3). The most affected areas include the Northern (Pomerania), Northeastern (Warmia and Mazuria), and the Southern (particularly the Carpathian region bordering Slovakia) parts of the country (Dubinsky et al., 2006; Reiterová et al., 2006; Borecka et al., 2008). The latest national epidemiological survey available has shown that *E. multilocularis* has expanded its geographical range and is now present in 14 of the 16 provinces in Poland at a mean prevalence of 16.5% (Karamon et al., 2014). A highly aggregated distribution pattern of the worm burden has been demonstrated in a previous study where only a small fraction (5%) of the infected foxes carried heavy loads (>1000 adult worms) of the parasite (Borecka et al., 2008). As in the case of Switzerland, it is now accepted that growing fox populations in Poland has been paralleled with increased number of *E. multilocularis* infected foxes and followed by increased number of human AE cases. Evidence from the existence of a synanthropic transmission cycle of the parasite comes from the recent finding of *E. multilocularis* metacestodes in the liver of pigs (Karamon et al., 2012), together with the report of at least three new Polish patients confirmed with AE in 2011 (EFSA, 2013). No studies documenting *E. granulosus* s.l. infections in wildlife species have been found, although 21 human isolates from subjects with confirmed CE have been characterized as *E. canadensis* G7 (see Alvarez Rojas et al., 2014). Considering that this genotype is known to be transmitted through a domestic cycle involving mainly pigs but also cattle in adjacent Lithuania and Slovakia (see Cardona and Carmena, 2013), it is most likely that human infections by *E. canadensis* G7 in Poland are also of domestic origin. The epidemiological status of canine echinococcosis in this country is currently unknown.

Slovakia is considered endemic for *E. multilocularis*. The most affected areas include those of the Northeast and the mountainous Central parts of the country. Following the same trend observed in adjacent countries (e.g. Austria, Czech Republic or Poland), the Slovak fox population has experienced a 3-fold increase during the period 1993–2002 (Dubinsky et al., 2006), contributing to the elevated prevalences (10–43%) of the parasite frequently reported in this definitive host species. *E. multilocularis* infections at variable rates have also been documented in racoon dogs and wolves (Table 3). Environmental variables including low mean annual temperature, high mean annual rainfall, and high humidity levels of soil have been identified as relevant

factors explaining, at least partially, the distribution of the parasite in Slovakia (Miterpakova et al., 2006). Recent studies have shown that *E. multilocularis* infections are over-dispersed in the fox population, with 21–25% of the infected animals carrying >1000 adult worms for an estimate of >30,000 eggs released per animal/day (Reiterová et al., 2006; Hurníková et al., 2009). This fact highlights the epidemiological relevance of heavily infected animals (super spreaders) that contribute the bulk of environmental contamination with parasite eggs. Synanthropic cycles of *E. multilocularis* are expected to exist in some regions, as suggested by the detection of adult worms of the parasite in domestic dogs (see Carmena and Cardona, 2013). No confirmed cases of human AE were reported in 2011 (EFSA, 2013), but the prediction is that new human cases will emerge in the near future. At present, no sylvatic cycles involving *E. granulosus* s.l. species are known to exist in Slovakia, although *E. canadensis* G7 is the only genotype documented in livestock species (see Cardona and Carmena, 2013) and humans (Alvarez Rojas et al., 2014).

Little information exists on the epidemiological situation of *E. multilocularis* in Romania. The parasite has been recently recorded in fox (infection rates: 5–18%) and small mammal populations from the North and Northwest regions of the country bordering Hungary and the Ukraine (Table 3). A total of 53 patients infected by *Echinococcus* spp. have been reported in Romania in 2011 (EFSA, 2013). Although the exact proportion of human AE cases is unknown, the vast majority of human CE cases are very likely caused by *E. granulosus* s.s. (Alvarez Rojas et al., 2014), as this *Echinococcus* species (and, to a much lesser extent, *E. canadensis* G7) is known to be circulating through a domestic cycle involving production animals and dogs (see Cardona and Carmena, 2013; Carmena and Cardona, 2013).

Since the dissolution of the former Soviet Union and due to the resulting disruption of veterinary and public health services, echinococcosis is considered to be re-emerging in Russia (Torgerson and Budke, 2003; Konyaev et al., 2013). A recent molecular study has confirmed the presence of the Asian genotype of *E. multilocularis* in a single isolate of a fox from the central part of the Russian Plain and a wolf from the South-Central region of the country bordering China, Kazakhstan, and Mongolia (Table 3). In the latter region, three vole isolates were additionally assigned to the Mongolian genotype of the parasite, whereas the European variant of *E. multilocularis* has been identified in a vole from the Moscow area (Konyaev et al., 2013). Taken together, these data demonstrate that *E. multilocularis* is ubiquitously circulating in a variety of sylvatic cycles in Russia and can even be found infecting synanthropic voles. Interestingly, all the human AE cases from the above mentioned areas that have been subjected to molecular characterization have been found to be the Asian genotype of *E. multilocularis* (Konyaev et al., 2012, 2013; Nakao et al., 2013b), strongly suggesting that a synanthropic cycle of the parasite is taking place in South-Central Russia. Canine echinococcosis epidemiological studies are needed to fully confirm this hypothesis. On the other hand, a sylvatic cycle of *E. canadensis* G6 has been documented between wolves and reindeer (Nakao et al., 2013b), and the same genotype has also been found in a human CE patient (Konyaev

et al., 2013). Whether this human infection is the result of direct contact with infected wild animals or domestic dogs participating in a peri-domestic transmission cycle of the parasite is still unclear. In Russia, *E. granulosus* s.s. has been reported infecting only domestic production animals and dogs, but not wild carnivorous. The epidemiological situation of echinococcosis in wildlife species from the North-Asian portion of Russia has been already discussed above (see Section 4.1).

In neighbouring Ukraine, *E. multilocularis* is present at low prevalence rates (2.4%) in foxes from the Western part of the country (Table 3). Failure to detect the larval stage of the parasite in small mammal populations and lack of reported human AE cases seems to indicate that the introduction of the parasite in the country is a recent event very likely linked to migrating fox populations from endemic areas of Hungary, Poland, Slovakia, or Romania (Kharchenko et al., 2008).

5.4. Echinococcosis in wild carnivorous from southern Europe

In Italy, *E. multilocularis* was detected for the first time in two foxes from an Alpine area near the Austrian border (Manfredi et al., 2002). Ensuing field surveys in the same region (Trentino Alto Adige) have confirmed the presence of the parasite in 4.8% of foxes, but not in foxes from the Valle d'Aosta, Liguria, Lombardy, and Veneto regions of Northern Italy (Casulli et al., 2005) or from the Apennine area of Central Italy (Calderini et al., 2009). This finding raised the question as to whether the infection constitutes a true local endemic focus that has remained undetected until 2002 or whether it has been introduced recently by migrating fox populations from Central Europe. Molecular studies based on microsatellite analyses have revealed that the Italian isolates of *E. multilocularis* were unique compared to other European and American isolates, supporting the hypothesis of an autochthonous focus of the parasite in Northern Italy (Casulli et al., 2009). No human AE cases have been officially reported in Italy in recent years. In addition, *E. granulosus* s.l. has been found infecting wolves in the Apennine Region at a prevalence rate of 15% (Table 3). Although no genotyping data were provided, it is believed that wolves acquired the parasite by preying on infected livestock species (Guberti et al., 2004). In this regard, it is important to mention here that *E. granulosus* s.s., *E. equinus*, *E. ortleppi*, and *E. canadensis* G7 are all known to be circulating through domestic cycles in Italy (see Cardona and Carmena, 2013).

In the Iberian Peninsula, wolves have also been found infected with *E. canadensis* G7 in Portugal and *E. granulosus* s.s. G1 in Spain (Table 3). No human or animal infections by *E. multilocularis* have been documented from these countries to date. Echinococcosis by *E. granulosus* spp. is endemic in Spain, where *E. granulosus* s.s., *E. equinus*, and *E. canadensis* G7 occur sympatrically and have been identified in a number of production animal species (Carmena et al., 2008). In addition, wild boars can harbour hydatid cysts by both *E. granulosus* s.s. G1 and *E. canadensis* G7 (González et al., 2002; Martín-Hernando et al., 2008), demonstrating that these genotypes are simultaneously transmitted

through domestic and sylvatic cycles in Spain. A very similar epidemiological scenario takes place in Portugal, where *E. granulosus* s.s. G1 and *E. canadensis* are known to occur in livestock species (Guerra et al., 2013). Whether *Echinococcus* spp. infection in Spanish and Portuguese wolves is the result of true sylvatic cycles or a spill-over event from a domestic cycle of the parasite is still a matter to be elucidated in further studies. In any case, wolves in these countries may act as natural reservoirs of the disease and, therefore, their potential contribution to human infection needs to be assessed.

A recent national epidemiological survey in Slovenia has detected the presence of *E. multilocularis* in 2.6% of the fox population (Table 3), most commonly in the southeastern part of the country (Rataj et al., 2010). Interestingly 67% of the infected animals from this particular region carried heavy loads (>1000 adult worms) of the parasite. The national annual incidence of infection per 100,000 human population for the period 2001–2005 has been estimated at 0.45 (Logar et al., 2007). In addition, eight new CE/AE (not specified) human infections were reported only in 2011 (EFSA, 2013). No data are available to assess whether these human infections are the result of direct contact with wild definitive hosts or have been acquired from infected domestic dogs.

No epidemiological information regarding the transmission of *Echinococcus* spp. in wildlife from Albania, Bosnia and Herzegovina, Croatia, Greece, Macedonia, Malta, Montenegro, and Serbia are currently available.

6. *Echinococcosis* in American wild carnivorous species

The geographical distribution of *E. multilocularis* in the Americas comprises the tundra zone of Alaska, North and South-Central Canada, and much of the North-Central and Midwestern United States. However, more recent epidemiological data have shown that the parasite has expanded its range of influence southward and eastward, and its prevalence has been increasing in wild canid populations (Kazacos, 2003; Moro and Schantz, 2006). The sylvatic transmission cycle of *E. multilocularis* is maintained between coyotes and foxes acting as definitive host species and a number of small rodents such as voles, mice, and muskrats serving as intermediate host species. However, an increasing urbanization of coyote populations has been recently observed in certain areas (Catalano et al., 2012). As already demonstrated in other countries such as China (see Section 4.5), France, Germany, and Switzerland (see Section 5.2) this finding may pose important veterinary public health consequence, as the establishment of *E. multilocularis* urban cycles may lead to accidental infection of domestic dogs and, subsequently, to increasing risk of AE transmission to humans.

Intraspecific genetic variation analyses of *E. multilocularis* isolates obtained in foxes and voles from Central USA have revealed a remarkable genetic homogeneity, clustering all together in what is now considered the North American genotype of the parasite (Nakao et al., 2009). A combination of North American and Asian *E. multilocularis* clades were also identified in Alaskan isolates from

the St. Lawrence Island in the Bering Sea, suggesting that this bridging area connecting North America and Asia has played a key role in the evolution and global geographic distribution of the parasite (Nakao et al., 2009). Coexistence of the Asian and North American haplotypes has been also documented in Russia (Konyaev et al., 2013). Despite the high prevalence and intensity of infection commonly reported in wild canids (see below), occurrence of human AE in North America seems rare, even in highly exposed population such as fox and coyote trappers in an endemic area (Hildreth et al., 2000). Indeed, only two cases of human AE have ever been confirmed in Central Canada and USA to date, suggesting that the North American genotype of *E. multilocularis* may pose little pathogenicity to humans (Davidson et al., 2012). This trend may be reverted in the near future if synanthropic cycles of the parasite are consistently established in North American conurbations.

Sylvatic cycles of *E. canadensis* G8–G10 are well known to occur in Alaska, Western Canada and North Central and Western states of USA, where the parasite is primarily transmitted between wolves and large wild ungulate (cervid) species (Kazacos, 2003). Domestic dogs may become infected through accidental consumption of fertile hydatid cysts within the viscera of affected cervids, and serve as source of infection to humans (Himsworth et al., 2010). *E. granulosus* s.l. is highly endemic in many areas of South America (see Cardona and Carmena, 2013; Alvarez Rojas, 2014), although the current status of the infection in wildlife is practically unknown. Regarding the Neotropical *Echinococcus* species, *E. vogeli* and *E. oligarthrus* are indigenous to the humid tropical forests in central and northern South America, being primarily transmitted in sylvatic cycles with bush dogs and wild cats as definitive host species and pacas and agouties as main intermediate hosts (D'Alessandro and Rausch, 2008). Although of very little clinical relevance, *E. vogeli* and *E. oligarthrus* are the etiological agents of human polycystic echinococcosis (PE) and human unicystic echinococcosis (UE), respectively.

6.1. *Echinococcosis* in wild carnivorous species from North America

In Canada, *E. multilocularis* and *E. canadensis* occur sympatrically. The former *Echinococcus* species has been found infecting coyotes in urban and peri-urban areas of Calgary and Edmonton (Alberta) at a prevalence rate of 25% (Table 4). Although the larval stage of the parasite has not been yet demonstrated in small rodent populations, the increasing presence of wild canids harbouring *E. multilocularis* adult worms in these urban settlements may constitute the first step in the establishment of stable urban transmission cycles of the parasite. In addition, *E. canadensis* G8–G10 is also endemic in the country and cycle between wild large cervids, primarily moose, and wild carnivores, primarily wolves (Thompson et al., 2006). Both G8 and G10 genotypes have been confirmed in wolf isolates from Alberta and British Columbia (Table 4). Evidence supporting the existence of synanthropic cycles of the parasite comes from the finding of adult worms of *E. canadensis* G10 in semi-stray dogs and the detection of an elevated human CE seroprevalence rate (11%) in an indigenous community

Table 4
Prevalence and molecular epidemiology of echinococcosis in American wild definitive host species (2000 onwards).

Country	Host species	No. samples ^a	Diagnostic procedure	<i>Echinococcus</i> species and prevalence (%)	Intensity of infection	Molecular characterization			Reference
						No. isolates ^c	Gene markers	Genotype frequency (%)	
Argentina	Fox	81	Necropsy	<i>E.g. s.l.</i> (1.2%)	1 ^b	–	–	–	Zanini et al. (2006)
Brazil	Bush dog	–	–	–	–	1 (AW)	<i>Ag4, cox1, Eg 10, ERK, Ir, P-29, Tgf cox1</i>	<i>E.v.</i> (100%)	Santos et al. (2012)
	Bush dog	–	–	–	–	1 (AW)		<i>E.v.</i> (100%)	do Carmo Pereira Soares et al. (in press)
Canada	Coyote	91	Necropsy	<i>E.m.</i> (25.3%)	20.5 ^b	23 (AW)	<i>nad1, rrnS</i>	<i>E.m.</i> (100%)	Catalano et al. (2012)
	Wolf	–	–	–	–	1 (AW)	<i>atp6, cox1, ITS1, nad1</i>	G10 (100%)	Thompson et al. (2006)
	Wolf	–	–	–	–	6 (E)	<i>nad1</i>	G8 (83.3%); G10 (16.7%)	Bryan et al. (2012)
	Wolf	93	Necropsy/SFCT	<i>E.c.</i> (26.9%); <i>E.m.</i> (12.9%)	2420	NS (AW)	<i>nad1</i>	<i>E.m.</i> (40.0%); G8 (80.0%); G10 (16.7%)	Schurer et al. (2014)
USA	Coyote	9	Necropsy	<i>E.m.</i> (44.4%)	NS	–	–	–	Hildreth et al. (2000)
	Coyote	61	Necropsy	<i>E.m.</i> (3.3%)	NS	–	–	–	Storandt and Kazacos (2012)
	Fox	137	Necropsy	<i>E.m.</i> (74.5%)	NS	–	–	–	Hildreth et al. (2000)
	Fox	125	Necropsy	<i>E.m.</i> (21.6%)	282	–	–	–	Storandt et al. (2002)
	Fox	176	Necropsy	<i>E.m.</i> (7.4%)	NS	–	–	–	Storandt and Kazacos (2012)
	Wolf	123	Necropsy	<i>E.g. s.l.</i> (62.6%)	NS	–	–	–	Foreyt et al. (2009)

Ag4: nuclear malate dehydrogenase; *atp6*: mitochondrial ATPase sub-unit 6; *cox1*: mitochondrial cytochrome c oxidase sub-unit 1; *E.c.*: *Echinococcus canadensis*; *E.g.*: *Echinococcus granulosus*; *Eg 10*: nuclear *E. granulosus* Eg 10 antigen; *E.m.*: *Echinococcus multilocularis*; *ERK*: nuclear extracellular signal-regulated kinase; *E.v.*: *Echinococcus vogeli*; *Ir*: nuclear insulin receptor; *ITS1*: ribosomal internal transcribed spacer 1; *nad1*: mitochondrial NADH dehydrogenase subunit 1; NS: not specified; P-29: nuclear *Echinococcus* P-29 antigen; PCR: polymerase chain reaction; *rrnS*: small subunit of ribosomal RNA; *Tgf*: nuclear transformig growth factor.

^a Number of definitive host individuals analyzed by necropsy.

^b Mean intensity of infection (mean number of adult worms per infected definitive host).

^c An isolate is defined here as parasite DNA extracted from *Echinococcus* adult worms (AW).

in South-Central Canada (Himsworth et al., 2010). Indeed, at least 19 human CE cases have been confirmed between 1991 and 2001 in the province of Alberta, most of them suspected to be caused by *E. canadensis* (Somily et al., 2005). This epidemiological scenario would suggest a spill-over situation from sylvatic to domestic transmission cycles of the parasite.

As in the case of Canada, *E. multilocularis* and *E. granulosus* s.l. also occur sympatrically in neighbouring USA. The geographical distribution of *E. multilocularis*, initially circumscribed to the North-Central region of the country, has now expanded to the states of Montana, Eastern Wyoming, and North-Central Ohio, and it is expected to continue to the east and south. Increasing infection rates of the parasite have been found in coyote (3–44%) and fox (7–74%) populations (Table 4) in a number of epidemiological field surveys carried out in Michigan and Ohio (Storandt and Kazacos, 2012), South Dakota (Hildreth et al., 2000), and Nebraska (Storandt et al., 2002). Despite the increase in geographic range of the coyote and fox populations, urbanization phenomena have not been reported in USA to date, suggesting that the likelihood of the existence of *E. multilocularis* synanthropic transmission is low at present. In addition, very high prevalence rates of *E. granulosus* s.l. have been found in wolves from the states of Idaho and Montana (Table 4), where 53% of the infected animals were carrying >1000 adult worms of the parasite (Foreyt et al., 2009). Suitable intermediate host species in the region include elk, deer, and mountain goat. Lack of molecular data does not allow assigning the exact genotype of the parasite involved in the infections. However, livestock CE and canine echinococcosis seem absent in Idaho and Montana (Moro and Schantz, 2006), suggesting that a true sylvatic of *Echinococcus* s.l. exists in the region.

6.2. Echinococcosis in wild carnivorous species from Central America

Two species, *E. vogeli* and *E. oligarthrus* occur in the humid tropical forests of Central America (D'Alessandro and Rausch, 2008). *E. vogeli* is primarily transmitted in the wild, where bush dogs are the only known natural final host, and pacas serve as intermediate host. Because pacas are extensively hunted for human consumption and domestic dogs are often fed their infected raw viscera, the parasite may circulate also in a synanthropic cycle. Consequently, domestic dogs are believed to be the most likely source of the comparatively rare human PE cases reported in Costa Rica ($n=1$), Ecuador ($n=11$), Nicaragua ($n=1$), and Panama ($n=2$) until 2007 (D'Alessandro and Rausch, 2008). On the other hand, *E. oligarthrus* is capable of development in any species of felid in the Neotropical region, including cougars, jaguars, jaguarundis, and ocelots. Suitable intermediate host species include agouties and pacas (D'Alessandro and Rausch, 2008). No human UE or canine infections have been reported in this geographical region to date, although at least four human UE cases have been documented in South America (see below). Finally, *E. granulosus* s.l. is thought to be infrequent or non-existent

in most countries of Central America (Moro and Schantz, 2006).

6.3. Echinococcosis in wild carnivorous species from South America

In Argentina, *E. granulosus* s.l. has been found in a single fox from Tierra del Fuego in the Southern part of the country (Zanini et al., 2006). Because livestock CE is highly endemic in this country (see Cardona and Carmena, 2013), it was assumed that access to sheep viscera containing fertile hydatid cysts was the most plausible explanation for the acquisition of the infection. Furthermore, *Echinococcus* hydatid cysts assigned to *E. vogeli* have been recently confirmed in a paca from the province of Misiones in the Northeastern corner of the country near the border with Paraguay and Brazil (Vizcaychipi et al., 2013). The presence of the natural definitive host species of the parasite, the bush dog, have also been documented in the same region, although no infected animals have yet been recorded. These findings, combined with the report of 11 human PE cases in Argentina until 2007 (D'Alessandro and Rausch, 2008), strongly suggest the occurrence of sylvatic and synanthropic cycles of the parasite in Argentina.

In Brazil, *E. vogeli* is transmitted in a natural life cycle involving bush dogs and pacas/armadillos (Table 4). Based on mitochondrial and nuclear DNA sequence polymorphism analyses of 19 human and 19 animal (13 pacas, five armadillos, and a single bush dog) isolates of *E. vogeli* from the Brazilian Amazon, it has been recently demonstrated that the cestode is partially synanthropic in this region, since identical genetic variants are found in wild animals and humans (Santos et al., 2012). A total of 98 human PE cases have been reported in Brazil until 2007 (D'Alessandro and Rausch, 2008). In addition, intraspecific genetic and geographic differences between *E. vogeli* populations from western and eastern Amazon have been also determined (Santos et al., 2012). Finally, at least two human UE cases have been documented in Brazil until 2012 (D'Alessandro and Rausch, 2008; Soares Mdo et al., 2013). Regarding *E. granulosus* s.l., no records of the present of these *Echinococcus* species infecting Brazilian wildlife have been found in the published literature.

Taking into consideration the epidemiological and molecular data from Argentina and Brazil, the fact that a number of human PE cases have also been described in Chile ($n=1$), Colombia ($n=29$), Peru ($n=1$), Surinam ($n=8$), Uruguay ($n=2$), and Venezuela ($n=3$) seems to indicate that *E. vogeli* is primarily transmitted through sylvatic cycles, although peri-domestic cycles may be also locally possible in these countries (D'Alessandro and Rausch, 2008). Two additional human UE cases have been identified in Surinam and Venezuela, respectively (D'Alessandro and Rausch, 2008).

7. Echinococcosis in Australian wild carnivorous species

E. granulosus s.s. is the only *Echinococcus* species present in Australia. The parasite is thought to have been accidentally introduced at the time of European settlement

in late 18th and early 19th centuries, spreading quickly in the fast-growing livestock and dog populations (Jenkins and Macpherson, 2003). The spill-over of *E. granulosus* s.s. into Australian wildlife was very likely initiated by dingoes preying on infected sheep, a process greatly enhanced by the transhumant grazing practices in place until mid-1970s (Jenkins and Morris, 2003). Successful consolidation of sylvatic transmission cycles of *E. granulosus* in Australia was only possible due to the presence of susceptible native canid predators (dingoes, feral dogs, and foxes) and their macropodid marsupial prey (kangaroos, wallabies, and wombats). Feral pigs can also act as suitable intermediate host species locally or sporadically (Banks et al., 2006; Jenkins, 2006; Jenkins et al., 2000). Such is the easy spread of the infection in the wild that wildlife is currently considered the main source of echinococcal infection to domestic animals and humans in Australia. Most affected regions include Victoria, New South Wales, and Queensland in the Eastern part of the country, and water-catchment areas outside Perth in Western Australia, although domestic cycles of the parasite are widespread except in the desert area of Central Australia (Jenkins and Macpherson, 2003).

By far, dingoes constitute the most important definitive host in the transmission of *E. granulosus* s.s. in the country, with infection ranges ranging from 22% to 100% (Table 5). Of great epidemiological relevance is the fact that the worm burdens of infected animals are remarkably high, with intensity of infections greater than 50,000 worms occurring frequently (Jenkins and Morris, 2003; Table 5). These figures illustrate the level of environmental contamination with parasite eggs that should be expected in endemic areas, providing a constant source of infection to production animals and humans. Foxes can also be infected by *E. granulosus* s.s., although the reported prevalence (19%) and intensity of infection rates (1–54 worms) are much lower than those documented in dingoes (Jenkins and Morris, 2003). Taking together, these facts seem to indicate that foxes are a much less important definitive host than dingoes in the sylvatic transmission of the parasite.

As in other parts of the world, urbanization of wild canid population is also a recent phenomenon in Australia. Dingoes and foxes have been increasingly seen scavenging for food, preying on domestic pets and livestock, and defaecating in gardens in a number of urban or sub-urban areas. More worryingly, dingoes wandering in newly developed settlements of the city of Townsville (North-eastern coast of Queensland) have been found infected with *E. granulosus* s.s. at a prevalence rate of 22% (Brown and Copeman, 2003). Similarly, adult worms of the parasite have been also detected in 46% of dingoes in two independent areas of the coast of Queensland (Jenkins et al., 2008). Foxes from the same areas were free of the infection. These findings clearly show that contamination of urban and sub-urban environments (including gardens and public parks) with dingo faeces may constitute a source of infection to humans. Based on the current data, establishment of urban transmission cycles of the parasite seems highly unlikely due to the absence of suitable intermediate hosts. In this regard, human CE cases are known to occur regularly in Australia. Although the infection is under-reported nation-

Table 5
Prevalence and molecular epidemiology of echinococcosis in Australian wild definitive host species (2000 onwards).

Host species	No. samples ^a	Diagnostic procedure	Echinococcus species and prevalence (%)	Intensity of infection	Molecular characterization		Reference
					No. isolates	Gene markers	
Dingo	23	Necropsy	<i>E.g.</i> s.s. (100%)	2–42,600	–	–	Jenkins et al. (2000)
Dingo	27	Necropsy	<i>E.g.</i> s.s. (22.2%)	<1000	–	–	Brown and Copeman (2003)
Dingo	221	Necropsy	<i>E.g.</i> s.s. (64.7%)	10–309,750	–	–	Jenkins and Morris (2003)
Dingo	21	Necropsy	<i>E.g.</i> s.s. (76.2%)	NS	–	–	Banks et al. (2006)
Dingo	108	Necropsy	<i>E.g.</i> s.s. (46.3%)	30–104,000	–	–	Jenkins et al. (2008)
Fox	129	Necropsy	<i>E.g.</i> s.s. (18.6%)	1–54	–	–	Jenkins and Morris (2003)

NS: not specified.

^a Number of definitive host individuals analyzed by necropsy.

wide, about 85 new cases were recorded annually during the period 1996–1999 (see Jenkins and Macpherson, 2003). Due to the elevated amount of infection found in wildlife, it has been speculated that a significant proportion of the human CE cases reported in Australia were derived from dingoes, although the exact proportion is currently unknown (Jenkins and Macpherson, 2003).

Finally, *E. granulosus* s.s. was previously widespread in domestic animals and humans in New Zealand and Tasmania. Because wildlife was never involved in the transmission pattern of the parasite, control efforts have succeeded and both regions are now considered *Echinococcus*-free (see Jenkins and Macpherson, 2003).

8. Concluding remarks

It is now broadly recognized that human health, animal health, and environmental health are inextricably linked and dynamically interdependent. The relevance of this phenomenon is clearly illustrated by the resurgence in recent years of infectious diseases of zoonotic origin responsible for a major morbidity/mortality burden worldwide. It is, therefore, not surprising the increasing attention that wildlife has received as natural reservoir of infection to humans and domestic animal populations.

Echinococcosis, one of the 17 neglected tropical diseases listed by the World Health Organization, is a zoonotic infection endemic, emerging or re-emerging in many areas of the world. As shown in this review, the epidemiology of *Echinococcus* spp. is complex and involves a variety of domestic, synanthropic, and wildlife cycles. Based on current epidemiological and molecular evidence, it seems clear now that *E. canadensis* G8–G10, *E. felidis*, *E. multilocularis*, *E. shiquicus*, *E. oligarthrus*, and *E. vogeli* are primarily transmitted through a number of sylvatic cycles specifically adapted to exploit with maximal efficiency any suitable hosts available in a given ecosystem under a given set of environmental conditions. Although *E. canadensis* G8–G10, *E. multilocularis*, *E. oligarthrus*, and *E. vogeli* have been demonstrated to cause human infections, it remains to be evaluated whether *E. felidis* and *E. shiquicus* are pathogenic to humans.

Human activity and intervention may greatly influence the transmission pattern of echinococcosis in a variety of ways. Human population growth and expansion into new geographic areas has led to encroachment on shrinking natural habitats, increasing the likelihood of contact with wild carnivorous harbouring *Echinococcus* infection and, therefore, the establishment of synanthropic cycles of the parasite. Examples of wildlife/livestock/human interfaces are particularly evident in some African countries, Australia, Brazil, and China. In these overlapping areas, wildlife may also become infected with domestic genotypes of the parasite (e.g. *E. granulosus* s.s.) as a consequence of spill-over events from domestic to sylvatic cycles. Infected wild animals may then act as reservoir of future infection to livestock and humans. In the latter scenario, control of the infection is greatly hindered and eradication judged unfeasible, as illustrated by the Australian case.

Another clear example of human intervention is the fox vaccination campaigns against rabies launched in

Western Europe during the late 1970s and early 1980s that led to the recovery of fox populations, which since then have expanded its geographical range and colonized new habitats, including urban settlements. Urbanization of fox populations has originated the establishment of well documented synanthropic transmission cycles of *E. multilocularis* in some French and Swiss cities, a phenomenon usually associated with higher risk or human AE cases. Likewise, migration of infected coyotes and wild dogs into urban settlements has been recently reported in Canada, USA, and Australia, suggesting that a similar epidemiological situation may occur shortly afterwards in certain areas of these countries.

Disruption of local environmental conditions by deforestation and agricultural practises has also a profound effect in the epidemiology of *Echinococcus* spp. For instance, by reducing biodiversity and favouring outbreaks of suitable intermediate host species, grasslands have been correlated with increased transmission of *E. multilocularis* in China and Central Europe. Uncontrolled international trade and translocation of wildlife animals may also pose important consequences if unnoticed infected animals from endemic areas are introduced or released into *Echinococcus*-free areas. This situation highlights the convenience of implementing effective international veterinary border control measures to minimize the risk of accidental introduction of the disease. In this regards, national wildlife disease surveillance schemes are a valuable tool to monitor the status of the infection or to early detect its accidental introduction.

Despite the progress achieved in the last decades, a number of issues related to the epidemiology of echinococcosis in the wild need further clarification. The status of the infection on the wildlife of many regions and countries is still unknown or poorly understood. Clearly, more field research should be done to complete our knowledge on the whole range of definitive and intermediate host species involved in the sylvatic cycles of *Echinococcus* spp. worldwide. Molecular data are also essential to estimate genotype frequencies of the parasite, to corroborate sympatric occurrence of different species in a given region, to determine zoonotic potential and phylogeography, and to demonstrate unambiguously the existence of spill-over events and their directionality in wildlife/livestock/human interfaces. All this information would prove useful not only to ascertain the host range and specificity of the parasite, but also to characterize its transmission dynamics in a given epidemiological scenario, and to design and implement effective control measures against the infection. Finally, and following the ‘One Health’ approach, it should be emphasized that successful veterinary public health interventions will be only achieved adopting a holistic approach that promote the collaborative effort of experts from different disciplines including human and animal medicine, public health, ecology, environmental sciences, and health economics.

Conflict of interest

The authors declare that there is no conflict of interest.

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