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Wilderness in the 'city' revisited: different *urbes* shape transmission of *Echinococcus multilocularis* by altering predator and prey communities

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The urbanization of *Echinococcus multilocularis*, the agent of alveolar echinococcosis (AE), is a public health concern worldwide. Here we propose to consider 'urban' habitats under a broad ecological perspective and discuss the effects of human settlements (*urbes*) on host communities and the process of parasite urbanization. We argue that interactions between landscape features (i.e., landscape composition and configuration) and host communities can shape the heterogeneity of transmission gradients observed within and across different types of human settlement. Due to unique ecological characteristics and public health management priorities, we envisage urban landscapes as a model system to further increase our understanding of host–parasite interactions shaping the circulation of *E. multilocularis*.

The urbanization and emergence of *E. multilocularis*

Urbanization has broad effects on ecosystem biodiversity [1], ecological mechanisms [2,3], and disease dynamics [4]. Exploring its effects on host–pathogen interactions becomes particularly interesting for trophically transmitted parasites, given the complex life cycles often involving intermediate and definitive host species with very different ecologies [5].

The cestode *E. multilocularis* is the causative agent of AE in humans, which is among the most serious emerging parasitic zoonoses for the Northern Hemisphere (case fatality rate >90% when untreated [6]). According to a 2014 report of the World Health Organization (WHO) and the United Nations' Food and Agriculture Organization (FAO), *E. multilocularis* is ranked as the food-borne parasite with the third greatest global impact [7]. Several interacting factors are possibly responsible for the parasite's global emergence [8]: (i) increases in definitive host populations [9,10]; (ii) landscape changes outside cities (e.g., deforestation, grassland extension) that promote high densities of intermediate host populations in endemic areas [11–13]; (iii) the inclusion of domestic animals into the parasite cycle and their role in parasite transmission to humans [14–16]; and (iv) the sprawl of cities into carnivores' natural habitats [17], along with growing trends in planning green spaces within urban landscapes [18].

The circulation of *E. multilocularis* in urban settings not only changed our perception of the risk of zoonotic transmission [10] but also generated new questions on the evolution of a complex ecological system. Yet, ecological mechanisms underlying the urbanization of parasites remain poorly understood. Seminal contributions to the understanding of the urban transmission of *E. multilocularis* come from research done in European cities [10,19,20], but there is a need to extend the concept of 'urban' to include other landscapes and types of human settlement (Table 1) where ecological processes [21] and control strategies [16,22] may be significantly different.

As a decade has passed since Deplazes *et al.* [10] published the first and only review focusing on urban *E. multilocularis* transmission, we here aim to: (i) revisit and broaden the concept of urban landscapes (including small human settlements in rural landscapes) in relation to the urbanization of *E. multilocularis*, in light of the evidence obtained in the past 10 years of ecological studies; and (ii) describe how the urbanization process affects key changes in intermediate and definitive host communities, their interactions, and, consequently, *E. multilocularis* transmission within and in proximity to urban settings.

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Table 1. Field-based research on *Echinococcus multilocularis* in urban habitats, excluding review papers

			Definitive host[c]			Intermediate host[5]	
Urban setting[a]	Location[b]	Study object	Species	% Prevalence in intestines	% Prevalence in feces	Species (% prevalence, *n*)	Refs
High-density city	Zurich (CHE)	Prevalence	*Vulpes vulpes*	36		*Arvicola sherman* (14%, 135)	[46]
High-density city	Zurich (CHE)	Prevalence	*V. vulpes*		25.8[1]	*A. sherman* (9.1%, 889)	[50]
High-density city	Zurich (CHE)	Prevalence				*Myodes glareolus* (2.4%, 83)	[50]
High-density city	Zurich (CHE)	Control	*V. vulpes*		n/a	*A. sherman* (6.8%, 1229)[3]	[69]
High-density city	Geneva (CHE)	Prevalence	*V. vulpes*	31			[70]
High-density city	Zurich (CHE)	Ecology	*V. vulpes*	16.5		*A. sherman* (n/a)	[19]
High-density city	Geneva (CHE)	Prevalence	*V. vulpes*	48.8			[29]
High-density city	Nancy (FRA)	Prevalence	*V. vulpes*	4			[20]
High-density city	Nancy (FRA)	Epidemiology	*V. vulpes*				[71]
Low–medium-density city	Sapporo city (JPN)	Prevalence	*V. vulpes*		21.3[1]	*Myodes rufocanus* (0%, 3)	[28]
Low–medium-density city	Sapporo city (JPN)	Prevalence	*V. vulpes*		16–49[1,2]		[72]
Low–medium-density city	Calgary (CAN)	Prevalence	*Canis latrans*	25.6	≤6.1[2]		[73]
Low–medium-density city	Calgary, Edmonton (CAN)	Prevalence	*C. latrans*	25.3			[17]
Low–medium-density city	Calgary (CAN)	Ecology	*C. latrans*		21.4[2]	*Peromyscus maniculatus* (0.66%, 310)	[21]
Low–medium-density city	Calgary (CAN)	Ecology				*Microtus pennsylvanicus* (0.75%, 267)	[21]
Low–medium-density city	Calgary (CAN)	Ecology				*Myodes gapperi* (1.41%, 71)	[21]
Low–medium-density city	Calgary (CAN)	Ecology/ epidemiology	*C. latrans*	25.0[4]			[74]
Low–medium-density city	Calgary (CAN)	Ecology/ epidemiology					[75]
Rural town	Koshimizu (JPN)	Control	*V. vulpes*		38.7–13.3[2]		[76]
Rural town	Abashiri, Nemuro, Kushiro (JPN)	Prevalence	*V. vulpes*	4		*M. rufocanus* (n/a)	[26]
Rural town	Nemuro City (JPN)	Control	*V. vulpes*	49.4[3]			[22]
Rural town	Otaru, Koshimizu, Nemuro (JPN)	Control	*V. vulpes*				[77]
Rural town	Otaru, Koshimizu, Nemuro (JPN)	Control	*Canis lupus familiaris*	0.4[1,2]			
Rural town	Otaru city (JPN)	Prevalence	*V. vulpes*	56.7			[59]
Rural town	Otaru city (JPN)	Prevalence	*Nyctereutes procyonoides*	23.1			[59]
Rural town	Chenaran county (IRN)	Prevalence	*V. vulpes*	10–22.9		*Ochtona rufescens* (75%, 4)	[80]
Rural town	Chenaran county (IRN)	Prevalence	*Canis aureus*	16		*Microtus transcaspicus* (29.6%, 54)	[27,78–81]
Rural village	Oberammergau and Starnberg (GER)	Prevalence/ ecology	*V. vulpes*	41.9–45.5	26.1[2]		[25]
Rural village	Zang county (CHN)	Epidemiology	*C. l. familiaris*	10			[82]
Rural village	Tuanji, Shiqu county (CHN)	Ecology				*Microtus limnophilus* (14.7%, 34)	[83]
Rural village	Shiqu county (CHN)	Ecology	*C. l. familiaris*	13–33		*Cricetulus kamensis* (5.3%, 19)	[41]
Rural village	Savoonga, St. Lawrence Island (USA)	Control				*Microtus oeconomus* (22–35%, n/a)[3]	[40]
Rural village	Shiqu county (CHN)	Ecology	*C. l. familiaris*		23[2]		[43]