

Trends in Parasitology

The 'bridge effect' by intermediate hosts explains differential distributions of *Echinococcus* species.

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Abstract:	Zoonotic cestodes in the genus <i>Echinococcus</i> show marked differences in their distribution patterns, which have not been satisfactorily explained. <i>Echinococcus multilocularis</i> is limited to moist and cool areas of the Holarctic, whereas species in the <i>Echinococcus granulosus sensu lato</i> (s.l.) complex mostly have a worldwide distribution encompassing hot and arid areas. We proposed and tested a 'bridge effect' hypothesis stating that the low virulence of species in the <i>E. granulosus</i> s.l. complex for their intermediate hosts and a longer lifespan of infected hosts explain the differential distributions. Human-mediated dispersal and egg shedding by definitive hosts might also be involved. In the light of globalization and climate change, understanding the drivers of zoonotic parasites distribution is critical to prevent pathogen outbreaks.

1 HIGHLIGHTS

- 2 - Understanding the drivers of differential distributions in zoonotic parasites is essential to
3 prevent pathogen outbreaks under global change.
- 4 - Species in the *Echinococcus granulosus sensu lato (s.l.)* complex are mostly
5 cosmopolitan, occurring in a wide range of conditions, whereas *Echinococcus*
6 *multilocularis* is limited to wet and cool areas of the Holarctic.
- 7 - We developed the ‘bridge effect’ hypothesis, according to which the lower pathogenicity
8 of *E. granulosus s.l.* species for intermediate hosts with a longer lifespan determines the
9 observed distributional differences.
- 10 - A critical review of the literature provided extensive support for the ‘bridge effect’
11 hypothesis and confuted or did not support alternative hypotheses.

1 **OUTSTANDING QUESTIONS**

- 2 - What is the role of variations in prey community structure and predator feeding behavior in
3 shaping large-scale transmission patterns of *Echinococcus* species?
- 4 - Do longevity of adult tapeworms and egg shedding behavior by definitive hosts contribute to
5 bridge *Echinococcus granulosus sensu lato* through harsh conditions?
- 6 - Does the 'bridge effect' hypothesis apply to other parasites with a similar life cycle, i.e.,
7 transmitted within a predator-prey system and involving a free-living stage?
- 8 - How does the different sensitivity of *Echinococcus* species to prolonged hot and dry periods
9 influence their response to climate change and globalization?

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31 January 2022

Dear Editor,

Please find enclosed our manuscript entitled “The ‘bridge effect’ by intermediate hosts explains differential distributions of *Echinococcus* species” by Massolo A., Simoncini A. and Romig T. that we would like you to consider for publication in Trends in Parasitology.

Determining the drivers of range size in parasites is a central aim of parasite biogeography. Parasites in the genus *Echinococcus* have different patterns of distribution: while *E. multilocularis* is confined to the Holarctic region, species in the *E. granulosus s.l.* complex can survive in arid and hot conditions and often attain a global distribution.

Our work is the first to formulate a biological hypothesis for this biogeographical phenomenon. We postulate that the lower virulence of species in the *E. granulosus s.l.* complex for intermediate hosts with a longer lifespan (compared to *E. multilocularis*) allows them to overcome prolonged periods of adverse conditions inside the intermediate hosts. This enables survival in harsh ecosystems and favors the establishment over wide geographical areas. We formulate a set of competing hypotheses and review the available evidence on *Echinococcus* ecology to support or discredit the hypotheses.

This work aims to understand the basic drivers of large-scale distribution patterns in a genus of parasites causing zoonoses of high medical relevance. Hence, it provides useful insights to drive prevention and control efforts under climate change and globalization.

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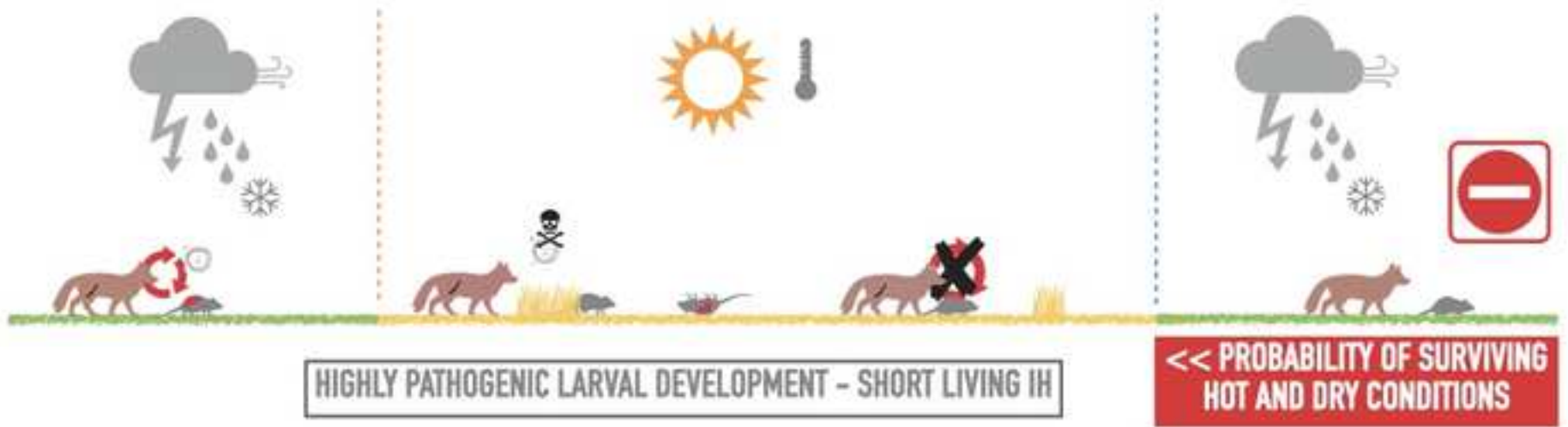
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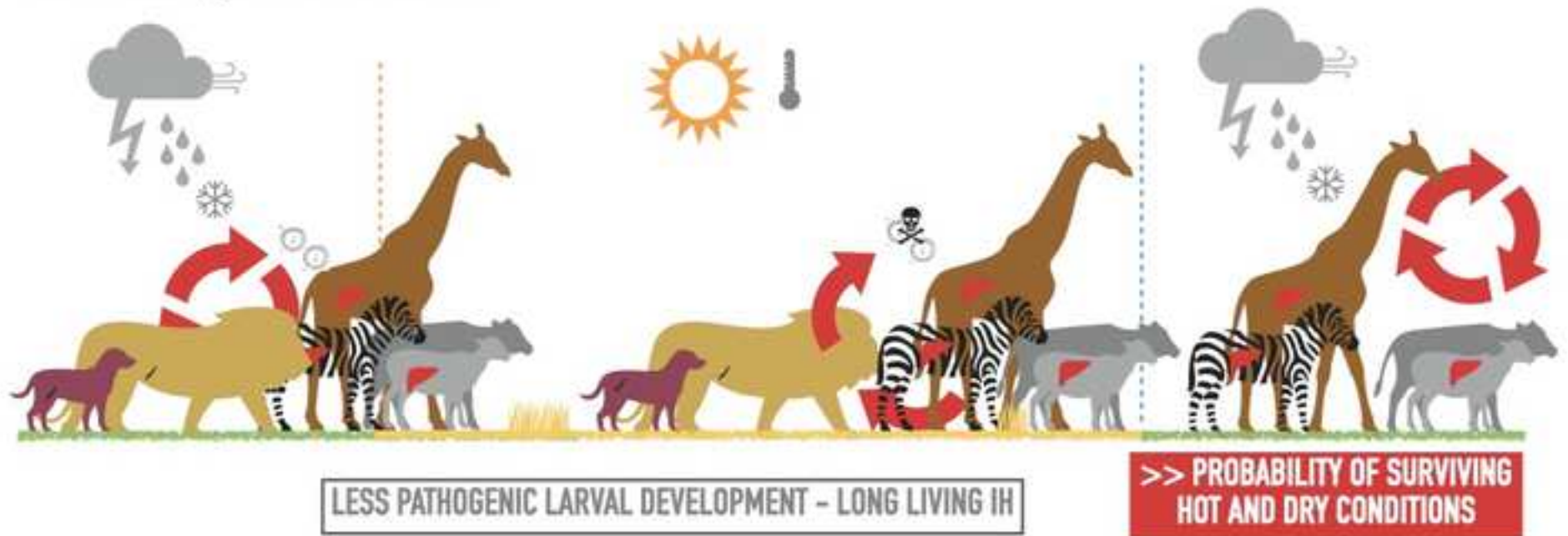
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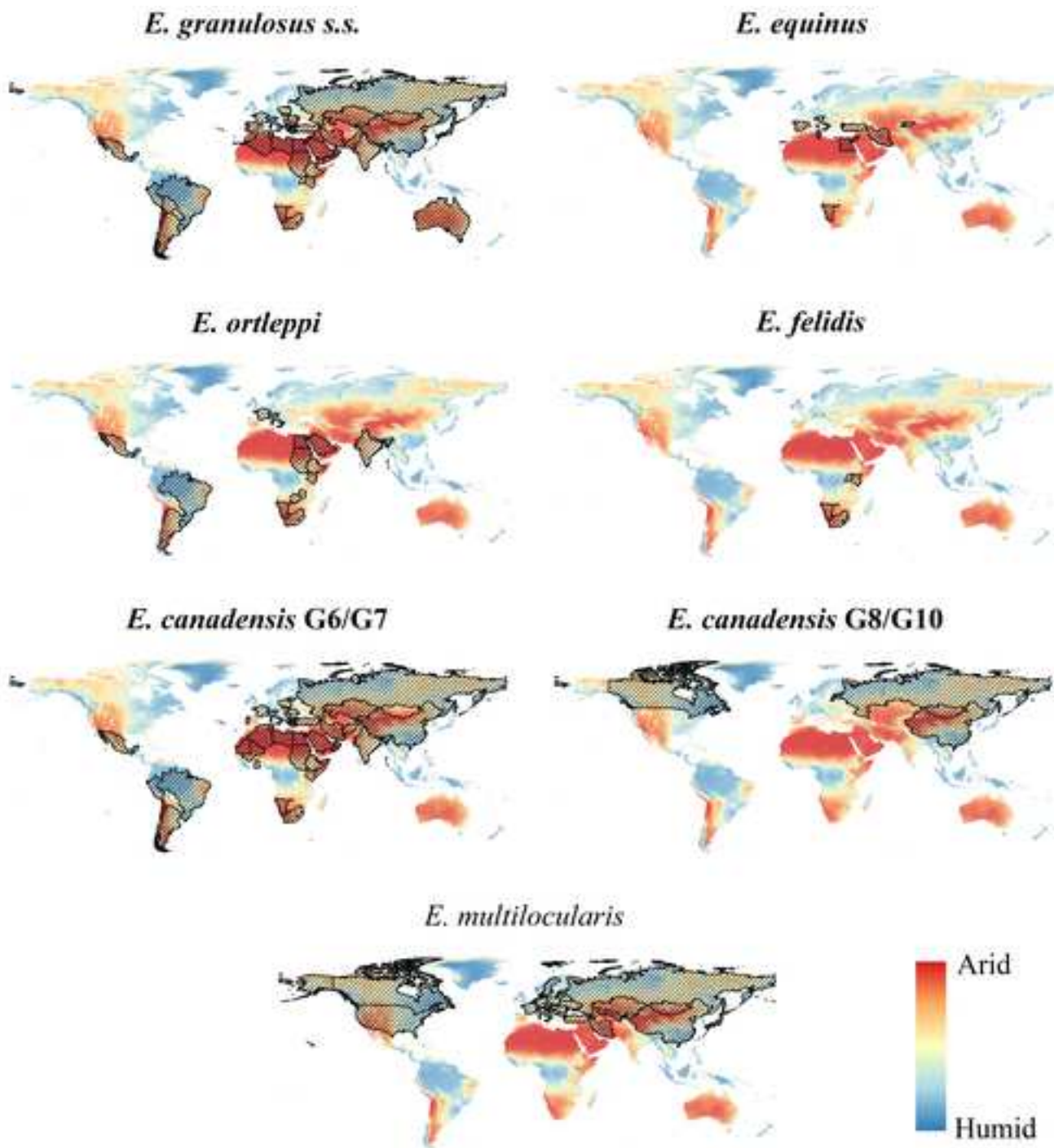
On behalf of the other co-authors

Echinococcus multilocularis



Echinococcus granulosus sensu lato





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1 **The ‘bridge effect’ by intermediate hosts explains differential distributions**
2 **of *Echinococcus* species**

3

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19 **ABSTRACT**

20 Zoonotic cestodes in the genus *Echinococcus* show marked differences in their distribution
21 patterns, which have not been satisfactorily explained. *Echinococcus multilocularis* is limited
22 to moist and cool areas of the Holarctic, whereas species in the *Echinococcus granulosus*
23 *sensu lato* (*s.l.*) complex mostly have a worldwide distribution encompassing hot and arid
24 areas. We proposed and tested a ‘bridge effect’ hypothesis stating that the low virulence of
25 species in the *E. granulosus s.l.* complex for their intermediate hosts and a longer lifespan of
26 infected hosts explain the differential distributions. Human-mediated dispersal and egg
27 shedding by definitive hosts might also be involved. In the light of globalization and climate
28 change, understanding the drivers of zoonotic parasites distribution is critical to prevent
29 pathogen outbreaks.

30

31 **Keywords:** *Echinococcus*; biogeography; distribution; intermediate host; virulence.

32 **BIOLOGY AND BIOGEOGRAPHY OF *Echinococcus***

33 *Echinococcus* is a genus of taeniid cestodes comprising nine species, one composed of a
34 genotypic cluster whose taxonomic status is debated [1,2]. They have complex life cycles,
35 circulating between carnivores (definitive hosts) and their prey (intermediate hosts). The
36 adults reproduce sexually in the carnivore's intestine and **eggs** (see Glossary) are released
37 with the last proglottids of mature worms into the intestinal lumen, and hence in the
38 environment with the faeces. The accidental ingestion of eggs by an intermediate host leads
39 to the release of **oncospheres** which will reach the target organs (most often liver and lungs)
40 and develop into **metacestode** larvae, reproducing asexually till the maturation of
41 **protoscoleces** [3]. Predation of an infectious prey by a competent definitive host completes
42 the cycle.

43 Humans become infected by occasional ingestion of eggs, acting as dead-end hosts [4]. Two
44 main zoonotic diseases are caused by parasites in this group: Cystic Echinococcosis (CE) and
45 Alveolar Echinococcosis (AE), causing a global burden of 1 million and 600.000 disability
46 adjusted life years, respectively [5,6].

47 Five species act as aetiological agents of CE and form the *Echinococcus granulosus sensu*
48 *lato (s.l.)* complex: *Echinococcus granulosus sensu stricto (s.s.)*, *Echinococcus equinus*,
49 *Echinococcus ortleppi*, *Echinococcus canadensis*, and *Echinococcus felidis* (Table 1) [7–9].

50 *Echinococcus granulosus s.s.* is the most widespread species within the group and is
51 responsible for most CE cases worldwide [8]. On the other hand, AE is caused by a single
52 species, *Echinococcus multilocularis* [6]. The causative agents of AE and CE also markedly
53 differ in their distribution patterns (Figure 1). While *E. granulosus s.l.* occurs throughout the
54 globe, *E. multilocularis* is limited to the Northern Hemisphere [10]. A central question in
55 parasite biogeography is why some species are able to attain a global distribution, whereas
56 others remain confined to certain regions [11]. Complex life cycle parasites are especially

57 sensitive to extreme climatic conditions, having longer generation times and slower
58 population growth rates than direct life cycle parasites [12]. Furthermore, the chance that a
59 phase or host of the cycle is affected by extreme events is higher [13]. Despite this, several
60 *Echinococcus* species survive and transmit successfully in harsh ecosystems, both in
61 extremely cold regions of the Arctic and in hot and dry regions of the Subtropics and Tropics.
62 However, there seem to be differences among *Echinococcus* species in the ability to cope
63 with extreme climatic conditions. In contrast to *E. multilocularis*, species of the *E.*
64 *granulosus s.l.* complex show a high endemicity in hot and dry areas across Africa, the
65 Mediterranean and Asia [10,14].
66 This ability of *E. granulosus s.l.* to survive in hot dry conditions and attain a far wider
67 distribution compared to *E. multilocularis* is as yet unexplained, and a full spectrum of
68 hypotheses has never been explored.
69 In this study we formally stated several competing hypotheses with their associated rationale
70 and prediction(s), and then critically reviewed the existing literature on *Echinococcus* in the
71 attempt to reject any of the postulated hypotheses.

72 **COMPETING HYPOTHESES**

73 For each hypothesis we provided a rationale, an unequivocal statement, and its consequential
74 measurable predictions.

75 ***H₁ - 'Bridge effect' by intermediate hosts***

76 Rationale. As hot and dry conditions are detrimental to the survival of eggs of all
77 *Echinococcus* species [15,16], transmission to intermediate hosts is reduced or interrupted
78 during droughts. Only the metacestodes of *E. granulosus s.l.*, characterized by a low
79 **virulence**, survive in long-lived infected intermediate hosts that 'bridge' the parasites through
80 such seasons. Instead, the transmission of *E. multilocularis* is prevented by the high virulence
81 of its metacestodes and the reduced longevity of the infected intermediate hosts [17].

82 Statement. The observed difference in range size and ability to colonize hot dry regions
83 between *E. granulosus s.l.* and *E. multilocularis* is explained by the lower virulence of larval
84 stages and the higher longevity of infected intermediate hosts in *E. granulosus s.l.* compared
85 to *E. multilocularis* (Figure 2, Key Figure).

86 Prediction(s). The virulence for intermediate hosts is higher in *E. multilocularis* and the
87 longevity of infected intermediate hosts is higher in *E. granulosus s.l.*

88 ***H₂ - Evolutionary history***

89 Rationale. Time since evolutionary origin has a strong influence on the geographical
90 distribution of organisms [18].

91 Statement. The observed difference in range size and ability to colonize hot dry regions
92 between *E. granulosus s.l.* and *E. multilocularis* is explained by an older origin of the former,
93 resulting in an increased time to spread over the globe.

94 Prediction(s). Representatives of the *E. granulosus s.l.* complex originated earlier than *E.*
95 *multilocularis*.

96 ***H₃ - Anthropogenic dispersal***

97 Rationale. Studies of *Echinococcus* **phylogeography** found a fingerprint of human-mediated
98 dispersal in the spatial genetic structure of species in the *E. granulosus s.l.* complex [7,19].

99 Statement. The observed difference in range size and ability to colonize hot dry regions
100 between *E. granulosus s.l.* and *E. multilocularis* is due to anthropogenic mobilization of hosts
101 for the former, allowing a rapid colonization of the globe in a short time.

102 Prediction(s). *E. granulosus s.l.* hosts are extensively moved around the globe via
103 anthropogenic means, and no species in the group colonizing hot dry regions has attained its
104 distribution via sylvatic hosts and without **spillovers** from domestic cycles.

105 ***H₄ - Intermediate hosts distribution***

106 Rationale. The distribution of *E. multilocularis* might be constrained by that of its main
107 intermediate hosts [20,21].

108 Statement. The observed difference in range size and ability to colonize hot dry regions
109 between *E. granulosus s.l.* and *E. multilocularis* is explained by the absence of suitable
110 intermediate hosts for the latter outside the Holarctic region.

111 Prediction(s). No suitable intermediate hosts for *E. multilocularis* exist outside the Holarctic
112 region or in non-endemic areas of this region.

113 ***H₅ - Host diversity***

114 Rationale. A wider host range increases the ability of parasites to spread over large areas
115 [22].

116 Statement. The observed difference in range size and ability to colonize hot dry regions
117 between *E. granulosus s.l.* and *E. multilocularis* is explained by a wider range of hosts in the
118 former.

119 Prediction(s). Species of the *E. granulosus s.l.* complex have a wider range of hosts
120 compared to *E. multilocularis*.

121 ***H₆ - Prey assemblages and prey selection by the definitive hosts***

122 Rationale. An effect of prey abundance and predator feeding behavior on spatial transmission
123 patterns has been ascertained for *E. multilocularis* [23,24].

124 Statement. The observed difference in range size and ability to colonize hot dry regions
125 between *E. granulosus s.l.* and *E. multilocularis* is explained by the altered transmission over
126 large areas of the latter in response to variations in prey assemblages and predator feeding
127 behavior.

128 Prediction(s). Variations of prey assemblages and predator feeding behavior correlate with
129 large-scale spatial patterns more in *E. multilocularis* than in the *E. granulosus s.l.* complex.

130 ***H₇ - Differential prepatent/patent periods and adult longevity***

131 Rationale. Longer **prepatent/patent periods** and increased longevity of adult *E. granulosus*
132 *s.l.* would allow to overcome prolonged adverse periods inside the definitive hosts.

133 Statement. The observed difference in range size and ability to colonize hot dry regions
134 between *E. granulosus s.l.* and *E. multilocularis* is explained by an increased time of
135 permanence and egg shedding in the definitive hosts for the former.

136 Prediction(s). Longevity of adults is higher and prepatent/patent periods are longer in *E.*
137 *granulosus s.l.* compared to *E. multilocularis*.

138 ***H₈ - Differential number of shed eggs***

139 Rationale. A larger number of eggs shed by the definitive host would increase the chance of
140 survival of some.

141 Statement. The observed difference in range size and ability to colonize hot dry regions
142 between *E. granulosus s.l.* and *E. multilocularis* is explained by an increased number of eggs
143 shed by the definitive hosts of the former.

144 Prediction(s). The total number of shed eggs is higher for the definitive hosts of *E.*
145 *granulosus s.l.* compared to the definitive hosts of *E. multilocularis*.

146 ***H₉ - Adaptations to high temperature and aridity***

147 Rationale. The adaptation of taeniid eggs to cold conditions has been assessed [25], and
148 similar adaptations might exist for warm and dry conditions.

149 Statement. The observed difference in range size and ability to colonize hot dry regions
150 between *E. granulosus s.l.* and *E. multilocularis* is explained by specific adaptations of *E.*
151 *granulosus s.l.* eggs providing a greater tolerance to high temperature and arid conditions.

152 Prediction(s). *E. granulosus s.l.* eggs possess a higher tolerance to high temperature and
153 aridity than eggs of *E. multilocularis*.

154 **SUPPORTING EVIDENCE**

155 *Evolutionary history and range dynamics*

156 *Echinococcus* began to diversify at the end of the Miocene 5.8 Mya (Million years ago) [26].
157 A **chronogram** of the genus [26] places the origin of *E. granulosus s.s.* and *E. multilocularis*
158 at 1.4 and 1.2 Mya, respectively, and the origin of the first representatives in the *E.*
159 *granulosus s.l.* complex at 3.9 Mya. However, the position of *E. multilocularis* in
160 *Echinococcus* phylogeny is debated [1,27]. Nonetheless, it appears that the genus is recent
161 and that species radiated rapidly, as the genetic relationships between members of the clade
162 are close [1,28]. *Echinococcus multilocularis* probably originated in the Beringia land bridge
163 in the Pleistocene (2.6 Mya - 11.7 kya), and subsequently spread through the Holarctic region
164 via the dispersal of its main definitive host, the red fox (*Vulpes vulpes*) [29]. A recent
165 expansion of *E. multilocularis* in Europe has been recorded since the 1990s as a result of
166 global change and the numerical increase and urbanization of red foxes [30,31].
167 *Echinococcus multilocularis* is also subject to extensive movement via human dispersal of
168 intermediate and definitive hosts, and has been introduced to several non-native countries
169 [32]. For instance, the European genotype was recently discovered in Canada, where it is
170 thought to have arrived via the introduction of red foxes or dogs from Europe [33].
171 *Echinococcus felidis* and *E. granulosus s.s.* might have originated in Asia from a common
172 ancestor [34]. Lions, the definitive host of *E. felidis*, probably originated in Asia and
173 subsequently spread to Africa, possibly carrying the cestode parasite with them [35,36].
174 Phylogeographic reconstructions for *E. granulosus s.s.* support the origin of this species in
175 the Middle East/eastern Mediterranean, and the following spread throughout the world via
176 livestock trade [2,19,37]. A similar influence of anthropogenic dispersal can be traced in the
177 G6/G7 genotypes of the *E. canadensis* cluster [7,38], in *E. equinus* and *E. ortleppi* [9,38,39].

178 Relevance for competing hypotheses

179 The rapid, recent radiation of *Echinococcus* species does not support our second hypothesis.
180 Despite the at least partially anthropogenic dispersal of hosts for *E. granulosus s.s.*, *E.*
181 *equinus*, *E. ortleppi* and *E. canadensis* G6/G7, *E. felidis* was able to colonize Africa through
182 a sylvatic transmission and the natural dispersal of its hosts. Furthermore, both *E. granulosus*
183 *s.l.* and *E. multilocularis* are subject to extensive human-aided dispersal, but only *E.*
184 *granulosus s.l.* could attain a global distribution. Hence, it seems that other factors are at
185 stake and that the third hypothesis should be mostly disregarded.

186 **Intermediate hosts distribution**

187 It was postulated that the distribution of *E. multilocularis* is limited by the presence of its
188 main intermediate hosts, i.e., microtine rodents, as these have a Holarctic distribution and the
189 parasite has never been found outside this region [20]. This hypothesis, involving a strict
190 host-specificity for the larval stage of *E. multilocularis*, is further supported by laboratory
191 experiments showing a lower susceptibility of murine rodents compared to the canonical
192 hosts [40]. A strong correlation was found between the distribution of *Microtus arvalis* and *E.*
193 *multilocularis* at the southern border of the known *E. multilocularis* distribution in Europe
194 [21]. However, *E. multilocularis* has been shown to perform **host switching** [41,42], and
195 numerous competent non-microtine intermediate hosts are known [4,43]. In the deserts of
196 Central Asia, suitable intermediate and definitive hosts are available across larger areas than
197 the restricted foci where *E. multilocularis* is found, typically near water sources [4,43].

198 Relevance for competing hypotheses

199 The available evidence suggests that, despite a local effect of intermediate hosts distribution
200 on *E. multilocularis* [21,44] possibly resulting from its adaptation to a locally dominant host
201 [4], *E. multilocularis* is able to infect many non-microtine intermediate hosts [42,43].

202 Furthermore, in dry regions the parasite is limited by factors other than the presence of
203 suitable hosts [43], invalidating our fourth hypothesis.

204 *Host diversity*

205 A positive correlation between the diversity of host range and the extent of occupied
206 geographical space is known [45]. *Echinococcus granulosus s.s.* has a wide variability in
207 infected hosts [4], and circulates in both domestic and sylvatic life cycles involving different
208 intermediate and definitive hosts according to the geographical location [4]. In contrast, two
209 species of the *E. granulosus s.l.* cluster are globally distributed, despite showing a narrow
210 intermediate host spectrum: *E. ortleppi* is well adapted to cattle, and *E. equinus* to species of
211 the horse family. *Echinococcus multilocularis* is able to infect a wide range of intermediate
212 and definitive hosts [4]. More than 40 small mammal species have been reported as
213 intermediate hosts for this cestode [4,46].

214 Relevance for competing hypotheses

215 Although relevant in general, host diversity does not seem so different between species
216 within *E. granulosus s.l.* and *E. multilocularis* to justify such differences in their
217 distributions, confuting the fifth hypothesis.

218 *Prey assemblages and prey selection by the definitive hosts*

219 In Canada, encounter rates of coyotes (*Canis latrans*) with *E. multilocularis* are modulated by
220 selective consumption of prey and the availability of non-competent prey [23]. Transmission
221 of *E. multilocularis* is reduced when the proportion of competent species within the prey
222 assemblage decreases [24], unless selective feeding of definitive hosts on competent species
223 occurs [23]. Furthermore, increased abundance of prey might result in a **dilution effect** and
224 decrease transmission [24].

225 No evidence of a strong correlation between *E. granulosus s.l.* transmission and prey
226 community ecology or predator feeding behavior exists.

227 Relevance for competing hypotheses

228 Variations in the composition of prey assemblages and in the prey selection behavior by the
229 definitive hosts influence *E. multilocularis* transmission on a local scale [23,24], but probably
230 fail to explain large-scale distribution patterns in the species [24]. Our sixth hypothesis
231 therefore cannot be confuted, although there is no support for it either. Thus, research on the
232 role of prey assemblages and feeding behavior of definitive hosts in shaping large-scale
233 transmission patterns of *Echinococcus* is required.

234 ***Infection in intermediate hosts***

235 *Echinococcus granulosus s.l.* typically infects ungulates [4], and larvae develop forming
236 single **hydatid cysts** in the liver and lungs [3,17]. After an asymptomatic phase, hosts might
237 be damaged by the pressure of cysts over vital organs [3,17]. However, the virulence for
238 intermediate hosts is typically low and infected hosts may live for long periods of time. For
239 instance, horses infected from at least 7, 11, 12 and 16 years have been reported, confirming a
240 high longevity of cysts in *E. granulosus s.l.* intermediate hosts [47]. In sheep, a longevity of 4
241 ½ years for infected individuals has been reported [48], whereas in Australian sheep it was
242 reported that cysts take 15 months or longer to reach fertility [49,50]. Unusually fast and
243 lethal infections of *E. granulosus s.s.* are known from macropods in Australia [4]. It must be
244 noted though, that these are phylogenetically unadapted hosts, as there is no indication that
245 the parasite had been endemic in Australia before the importation of livestock. An equally
246 unusual rapid onset of cyst fertility is noted for *E. canadensis* G7 in domestic pigs, which
247 might be a response of the parasite to the short lifespan of slaughter pigs [51]. However, there
248 is no indication that this early onset of fertility is linked to higher virulence to the host

249 animals. *Echinococcus multilocularis* typically infects rodents [4], and larvae undergo a
250 **multilocular development** often involving the establishment outside the liver and lungs [46].
251 This development in the intermediate host is rapid and typically leads to host death in a few
252 weeks from infection [17]. Apart from the different virulence, the longevity of intermediate
253 hosts for *E. granulosus s.l.* is remarkably higher compared to that of *E. multilocularis*
254 intermediate hosts [4]. The higher virulence of *E. multilocularis* might indeed reflect an
255 adaptation to short-lived hosts with a faster life history, probably linked to a high predation
256 pressure [3,52].

257 Relevance for competing hypotheses

258 Biological data clearly support our first hypothesis, providing evidence of higher virulence
259 and reduced longevity of infected hosts for *E. multilocularis*.

260 ***Infection in definitive hosts***

261 The **prepatent period** differs between *E. granulosus s.l.* and *E. multilocularis*. A prepatent
262 period of 35-45 days is mainly recorded for species of the *E. granulosus s.l.* complex [53],
263 although significant variation occurs based on species and strains, ranging from the 35 days
264 of *E. ortleppi* [54] to the 70 days of *E. equinus* [55,56]. The prepatent period is typically
265 shorter for *E. multilocularis*, with egg production beginning between 25 and 35 days after
266 infection [57,58]. The longevity of adult worms in the definitive hosts remains mostly
267 undefined [3], although five months is the estimated survival time of adult *E. granulosus s.l.*
268 [17]. A marked decrease in *E. multilocularis* burden from 35 to 63 days post infection was
269 demonstrated in red foxes [58], and a 95% reduction of the worm burden was described
270 during the first 27 days of the patent period [57]. Dogs, acting as relevant hosts in endemic
271 foci of China, Alaska and central Europe, might instead maintain a high worm burden after
272 90 days [31,59]. However, also in the case of dogs the main burden of *E. multilocularis* is

273 excreted in the first 43 days of the patent period [57]. In the case of *E. granulosus s.l.* in dogs,
274 most of the burden is released after the first month of the patent period [60].
275 The number of eggs produced per worm is higher for *E. granulosus s.l.* [3], with an average
276 number of 1503 (CIs 1173-1612) compared to 178 (CIs 158-210) of *E. multilocularis* [61]. *In*
277 *vivo* experiments [57] estimated the total number of excreted *E. multilocularis* eggs to be
278 346,473 (CIs 230,420–581,130) in red foxes.

279 Relevance for competing hypotheses

280 The available evidence, although not conclusive due to the paucity of studies in definitive
281 hosts, shows that the infection in definitive hosts is of limited duration. In fact, despite a
282 longer prepatent period in *E. granulosus s.l.* and a possibly long patent period for both *E.*
283 *granulosus s.l.* and *E. multilocularis*, the main worm burden decreases after a relatively short
284 time. No marked difference in the longevity of adult *E. granulosus s.l.* and *E. multilocularis*
285 has been clearly reported. Overall, our seventh hypothesis can be mostly confuted.
286 The higher number of eggs produced by species in the *E. granulosus s.l.* complex is
287 consistent with our eighth hypothesis. However, no clear indication on the total number of
288 excreted eggs for *E. granulosus s.l.* species is available. Hence, full support cannot be granted
289 to this hypothesis.

290 ***Ecological correlates of Echinococcus spp. presence***

291 Studies that relate environmental features to the occurrence of *E. granulosus s.l.* and *E.*
292 *multilocularis* in their natural hosts are numerous and provide important insights on
293 *Echinococcus* ecology.
294 In Germany, a positive correlation between moist areas in the vicinity of water courses and
295 prevalence of *E. multilocularis* in red foxes was reported [62]. In Central Asia, *E.*
296 *multilocularis* prefers areas around wetlands and at higher altitudes, avoiding hot and dry

297 areas [43]. Temperature and precipitation were major predictors of its occurrence in red foxes
298 in Hungary [63], and in Slovakia a positive correlation between prevalence in red foxes and
299 mean annual precipitation and a preference for low mean annual temperatures were described
300 [64]. The clumped distribution of *E. multilocularis* in intermediate hosts was described as an
301 outcome of the increased parasite survival near cold and humid areas [65]. A role of humidity
302 and rainfall on *E. granulosus s.s.* occurrence in dogs was found [66]. In Patagonia, *E.*
303 *granulosus* can withstand low precipitation amounts of 300 mm/year [67].

304 Relevance for competing hypotheses

305 Geographical correlation studies evidence a stronger influence of temperature and water
306 availability on *E. multilocularis*. Hence, either *E. granulosus s.l.* eggs have an increased
307 resistance to hot and dry conditions, enabling them to withstand a wider range of conditions
308 (ninth hypothesis), or the reduced virulence of the species for intermediate hosts combined
309 with the high longevity of the infected hosts allows the species to overcome prolonged
310 periods of adverse conditions in the larval stage (first hypothesis).

311 ***Egg adaptations to limiting environmental conditions***

312 *Echinococcus multilocularis* eggs are sensitive to high temperatures and desiccation (Table
313 2), and reduced egg survival following exposure to higher temperatures and drier conditions
314 has been proposed as a mechanistic explanation for the reduced abundance of the species in
315 the North Central Region compared to the Northern Tundra Zone in North America [33].
316 Eggs of *E. multilocularis* are highly resistant to cold temperatures, and can survive up to a
317 year in moist cool environments [17]; also *E. granulosus* sp. eggs can survive at cold
318 temperatures (Table 2). Possible adaptations of *E. multilocularis* and of some species of the
319 *E. granulosus s.l.* complex to cold environments are supported by the presence of both
320 throughout the Arctic region [68]. Moderate temperatures and sufficient moisture appear

321 critical for *E. granulosus s.l.* egg survival [17], and this is negatively correlated with
322 temperature (Table 2). Water might buffer the effect, as observed in the Turkana region of
323 Kenya where egg survival increased from two to 300 hours when eggs were located in water
324 bodies [69].

325 Relevance for competing hypotheses

326 Whereas eggs of both *E. multilocularis* and *E. granulosus s.l.* possess adaptations for
327 resistance to low temperatures, their survival is severely impaired by high temperatures and
328 desiccation. Therefore, support for our ninth hypothesis is scant.

329 **CONCLUDING REMARKS**

330 Explaining the factors responsible for range size is a central question in parasite
331 biogeography [11]. Species in the *E. granulosus s.l.* complex are able to survive in hot and
332 dry conditions and often attain a global distribution, whereas *E. multilocularis* is only found
333 in typically cold and wet areas of the Northern Hemisphere. We postulated that the higher
334 virulence of *E. multilocularis* for intermediate hosts with a shorter lifespan is primarily
335 responsible for the inability of the species to overcome hot and dry conditions, and in view of
336 the available evidence we could neither discredit this hypothesis, nor gather sufficient support
337 for any alternative hypothesis. Given the plausibility of our ‘bridge effect’ hypothesis, we
338 argue that a positive selection for transmission systems involving a lowered virulence for
339 long-lived intermediate hosts might intervene in hot and dry ecosystems. Despite the
340 increased resistance of *Echinococcus* eggs to low temperatures, severe cold conditions might
341 determine the patchy distribution of *E. multilocularis* throughout the Arctic [68], where a
342 ‘bridge effect’ by, e.g., reindeers (*Rangifer tarandus*), might explain the more widespread
343 distribution of *E. canadensis* G8/G10.

344 Our investigation was primarily concerned with the determinants of large-scale distribution
345 patterns. The fine-scale distribution of *Echinococcus* spp. is more likely driven by a complex
346 interplay of multiple factors [70], such as landscape and soil traits and the density of hosts'
347 populations [71]. Furthermore, host distribution *per se* can explain local scale distribution
348 patterns of the parasite [21], possibly as a result of adaptation to the most locally abundant
349 host species [4]. A role of prey community structure, predator feeding behavior and infection
350 in definitive hosts cannot be ruled out completely, given the inadequacy of current knowledge
351 on these topics (see Outstanding questions). Human-mediated dispersal, whose relevance for
352 *Echinococcus* species has been extensively reported [2,32], is a concurrent agent for the
353 establishment of realized distribution patterns, although it fails to explain their fundamental
354 ecological drivers. Given the relevance of this topic for general biogeography and for public
355 health [72], especially under globalization and climate change (see Outstanding questions),
356 we warrant further studies to quantitatively test our main hypothesis and its associated
357 predictions.

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359

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541 **GLOSSARY**

542 **Chronogram:** an evolutionary tree where the length of branches is proportional to time and
543 the age of nodes is reported.

544 **Dilution effect:** in parasites transmitted through predator-prey systems, a higher diversity of
545 prey that vary in their competence for a pathogen decreases infection prevalence in the
546 predators.

547 **Egg:** the structure comprising the embryo of *Echinococcus* worms and a series of layers and
548 membranes securing physical isolation and protection from the environment.

549 **Hydatid cyst:** the second stage of larval development in *Echinococcus granulosus sensu*
550 *lato*.

551 **Host switching:** a process where the host specificity of a parasite undergoes evolutionary
552 change, via the acquisition of traits that allow survival and transmission in a new host.

553 **Metacestode:** the second larval stage of tapeworms in *Echinococcus* worms, developing in
554 the viscera of an intermediate host.

555 **Multilocular development:** the development of metacestodes in *Echinococcus multilocularis*,
556 involving both endogenous and exogenous proliferation and the detachment of germinal cells
557 that are distributed in the blood or lymph.

558 **Oncosphere:** the first larval stage of tapeworms released when an egg hatches in the stomach
559 of an intermediate host and involved in the penetration of intestinal mucosa and the
560 movement through circulation to reach the viscera.

561 **Patent period:** the period in which eggs produced by the adult parasite are released in the
562 faeces of the definitive host.

563 **Phylogeography:** a discipline correlating relationships among genotypes with their spatial
564 distribution to infer the biogeographic history of a species or a group of closely related
565 species.

566 **Prepatent period:** the time occurring between the infection of a definitive host and the
567 release in the faeces of eggs produced by the adult parasite.

568 **Protoscolex (*plural: protoscoleces*):** the final larval stage of tapeworms, ingested by the
569 definitive host.

570 **Spillover:** the transmission of a parasite from one host species to another, that might or might
571 not result in the adaptation of the parasite to the new host.

572 **Virulence:** a measure of the severity of the disease induced in the host by an organism.
573
574

575 **Table 1.** Synopsis of *Echinococcus* species addressed in this review, their main hosts and
 576 geographical distribution.

577

Species	Strain/Genotype	Intermediate hosts	Definitive hosts	Distribution	Refs
<i>Echinococcus granulosus sensu stricto</i> ^a	Sheep/G1	Sheep, macropods, cattle, foxes	Dog, dingo	Worldwide	[1,4]
	Buffalo/G3	Buffalo, sheep	Dog	Worldwide	[1,4]
	G-Omo	?	?	East Africa	[9]
<i>Echinococcus equinus</i>	Horse/G4	Horse, donkey, plains zebra	Dog, lion, black-backed jackal	Worldwide (sporadic)	[1,4]
<i>Echinococcus ortleppi</i>	Cattle/G5	Cattle, goat, pig	Dog	Worldwide (sporadic)	[1,4]
<i>Echinococcus canadensis</i>	Camel/G6	Camel, goat, sheep	Dog	Worldwide	[1,4]
	Pig/G7	Pig, wild boar	Dog	Worldwide	[1,4]
	American' cervid/G8	Moose, domesticated reindeer	Wolves, dog	Northern arctic and boreal	[1,4]
	Fennoscandian' cervid/G10	Moose, domesticated reindeer	Wolves, dog	Northern arctic and	[1,4]

				boreal	
<i>Echinococcus felidis</i>	Lion	Warthog	Lion, spotted hyena	Sub-Saharan Africa	[1,4]
<i>Echinococcus multilocularis</i>	Four genotypes ^b	Voles, muskrat, lemmings, marmots	Foxes, raccoon, dog, jackal, wolf, dog, coyote	Holarctic	[1,4]

578

579 ^aSpecies in bold form the *Echinococcus granulosus sensu lato* complex. ^bAfter the original
580 description of three genotypes (North American, Asian and European), an additional
581 Mongolian genotype has been recently described [1,73].

582 **Table 2:** Evidence from experimental studies assessing *Echinococcus* species egg survival and
 583 infectivity under different environmental conditions.
 584

Species	Evidence	Refs
<i>Echinococcus multilocularis</i>	No infections after: 3 hours at 45°C (85-95% relative humidity); 2 hours at 43°C (15% relative humidity).	[74]
<i>Echinococcus multilocularis</i>	No infections after: 48 hours at -83°C; 20 hours at -196°C.	[74]
<i>Echinococcus multilocularis</i>	No infections after: 7.5 min at 80°C; 15 min at 75°C; 30 min at 75°C; 30 min at 70°C; 60 min at 70°C; 180 min at 65°C.	[15]
<i>Echinococcus granulosus</i> sp.	Eggs die immediately at 100°C and within 5 min at 60-80 °C.	[25]
<i>Echinococcus granulosus</i> sp.	Eggs exposed to -10, -20 and -30°C are as infectious as eggs exposed to 4°C, and after exposure to -50°C are still infective.	[25]
<i>Echinococcus granulosus</i> sp.	Egg survival drops from 225 to 21 days following a temperature increase from 6 to 30 °C.	[16]

585

586 **FIGURE LEGENDS**

587 **Figure 1. Distribution of *Echinococcus* species.** Reported countries of presence for
588 *Echinococcus multilocularis* and species in the *Echinococcus granulosus sensu*
589 *lato* complex (in bold) are shown against the Global Aridity Index map [75].
590 Genotypes of *E. canadensis* with domestic (G6/G7) and sylvatic (G8/G10) life
591 cycles are depicted separately. Data from [10,14].

592 **Figure 2. The ‘bridge effect’ hypothesis.** The high virulence of *Echinococcus multilocularis*
593 for short living intermediate hosts limits the ability to overcome hot and dry
594 conditions (higher panel). The low virulence of species in the *Echinococcus*
595 *granulosus sensu lato* complex for long living intermediate hosts allows to cross
596 hot and dry conditions (lower panel). IH = Intermediate Hosts.