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Review

Terrestrial invertebrate hosts of human pathogens in urban ecosystems

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ABSTRACT

Terrestrial invertebrates in urban ecosystems are extremely species-rich, have many important roles in material flow and energy circulation, and are host to many human pathogens that pose threats to human health. These invertebrates are widely distributed in urban areas, including both out- and in-door environments. Consequently, humans are frequently in contact with them, which provides many opportunities for them to pose human health risks. However, comprehensive knowledge on human pathogen transfer via invertebrates is lacking, with research to date primarily focused on dipterans (e.g., mosquitoes, flies). Here, we take a broad taxonomic approach and review terrestrial invertebrate hosts (incl. mosquitoes, flies, termites, cockroaches, mites, ticks, earthworms, collembola, fleas, snails, and beetles) of human pathogens, with a focus on transmission pathways. We also discuss how urbanization and global warming are likely to influence the communities of invertebrate hosts and have flow-on risks to human health. Finally, we identify current research gaps and provide perspectives on future directions.

1. Introduction

The ecological trade-offs inherent in urban ecosystems have emerged as one of the most challenging issues in urban planning, garnering significant attention from policymakers, sustainability practitioners, and conservationists. While urban green spaces are essential for providing ecosystem services, they also present risks by harboring potential human pathogens [1,2]. In terms of habitat diversity, urban environments offer rich and varied habitats for invertebrates. The soils within these urban green spaces serve as a home for a diverse array of invertebrates, playing a crucial role in ecosystem functionality [3]. Meanwhile, it is noteworthy that specific invertebrate species, particularly cockroaches and flies, predominantly rely on human-generated domestic waste for their survival [4] Invertebrates are present in basically all urban areas, including both indoor and outdoor environments. Their omnipresence results in frequent encounters with humans [5–7]. With human population models indicating that our urban population will reach five billion by 2030 [8], understanding human-invertebrate interactions are increasingly important.

Predominantly residing in soils, invertebrates are fundamental to sustaining urban biodiversity [9]. Their roles are diverse and essential, including pathogen control and soil quality enhancement [10]. However, urban invertebrates also introduce significant public health challenges by hosting pathogens detrimental to human health [11,12] (Fig. 1). Disease transmission from these organisms occurs through various mechanisms, including acting as mechanical vectors, biting, and contact with excreta [13]. The subtle nature of many of these interactions can often leads to people being unaware of human pathogen exposure [14].

Despite the well-documented health risks associated with specific invertebrates, like mosquitoes and flies, there is a noticeable gap in our understanding of a broader range of urban invertebrate species. Recent research has primarily focused on symbiotic microbial relationships within invertebrates, which has resulted in insufficient research on their role as hosts of human pathogens [15–17]. The *SARS-CoV-2* pandemic highlights the importance of understanding wildlife-human disease contact [18], including the role invertebrates play as potential human disease vectors. This lack of knowledge impedes the development and

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Fig. 1. Illustration of common terrestrial invertebrates and their potential interactions with humans and pets in urban settings.

implementation of effective disease control strategies, such as integrated vector management [19].

As urban landscapes continuously evolve, due in large part to intensifying urbanization, the dynamics between invertebrates, pathogens, and humans are also undergoing significant change. This further necessitates a greater understanding of these relationships, in the hope of more proactively manage and respond to human disease outbreak risks. Here we review urban terrestrial invertebrates and their human-associated pathogens. Through the adoption of a "hosts-pathogens-pathways-challenges" framework, this study aims to present a holistic view of the current knowledge, challenges, and potential future directions in this area.

2. Human pathogens carried by urban invertebrates

This section focuses on ten primary groups of terrestrial invertebrates in urban ecosystems selected for their ubiquity in urban zones and significant spatial intersection with human dwellings. Flies, often found in residences, exhibit a density correlating with the presence of sanitation and waste disposal facilities [20]. Mosquitoes are common in many urban spaces, including greenspaces, homes, and public infrastructure. The advent of urban farms has been identified as providing environments supportive of the proliferation of mosquitoes that are well-known human disease vectors [21]. The remaining nine groups (termites, cockroaches, mites, ticks, springtails, fleas, earthworms, snails, and beetles) are soil-affiliated and inhabit diverse soil ecosystems. These ecosystems range from private gardens and community green spaces to green roofs and walls and also include indoor potted plants and aerobiomes derived from both indoor and outdoor soils, including dust [22]. We would like to provide a concise and focused summary here rather than a wordy statement. Although taxa on the genus or class level are not strong evidence of human pathogens, we discuss it to explore the potential pathogenicity and future direction under the limitations of our current knowledge. While no clinical cases demonstrate the pathogenicity of soil fauna we have detected human-associated pathogens in the gut microbiome of such fauna, including earthworms and collembolans [23,24], finding them posing potential sources of pathogens. The comprehensive and detailed information, including hosts, pathogens, and diseases, is provided in Table 1 [16, 24–71] and Table 2. We highlight the urgent, novel, and neglected human pathogens and aim to expand the knowledge boundary.

2.1. Mosquitoes

In urban settings, especially in tropical regions, mosquitoes stand out as principal vectors for various human pathogens [72–75]. The mosquitoes *Aedes aegypti*, *Aedes albopictus*, and *Culex pipiens* complex are among the most important vector species found in urban areas due to their adaptation to breeding in man-made containers [76]. Mosquito-borne human diseases like dirofilariasis, West Nile virus, yellow fever, Chikungunya virus, dengue fever, and lymphatic filariasis have been extensively reviewed [77, 78] and are not further examined in this review.

2.2. Flies

Urban environments frequently host flies whose population densities often correlate with the presence of sanitation facilities, marked by clear seasonal variations [79]. A comprehensive review by Khamesipour et al. [80] highlighted more than 130 human pathogens, mainly carried by the housefly (*Musca domestica L.*). This review extends that knowledge by discussing additional urban fly species, offering deeper insights into fly-borne diseases.

Sandflies (Phlebotomines) have been identified as transmitters of the Toscana virus within the Mediterranean region [25]. It is important to note that in rare instances, flies have been documented carrying norovirus.

Sandflies also play a crucial role as vectors for *Leishmania*, which is responsible for severe diseases in humans. Various sandfly species, including *Phlebotomus kandelakii*, *P. perfiliewi*, and *P. alexandri* have been implicated in *Leishmania* transmission within Iran [81]. In central Tunisia, *P. perfiliewi*, *P. perniciosus*, and *P. longicuspis* (of the *Larrousse* subgenus) are primary vectors for *Leishmania* transmission. Furthermore, other fly-borne parasites like *Trypanosoma* sp. have been identified, with *Glossina pallidipes* Austen (Diptera; Glossinae) serving as a significant vector for African trypanosomiasis in East Africa, thereby causing a substantial number of infections in tropical regions [28]. *M. domestica* subsp. *vicina* is a carrier of *Balantidium coli* cysts, *Ancylostoma duodenale* eggs, *Enterobius vermicularis* eggs, and *Strongyloides stercoralis* larvae [36].

2.3. Termites

The gut microbiome of termites has garnered considerable attention and has been thoroughly studied [15]. König [82] identified spore-forming bacteria and *Paenibacillus* in termite guts. Further studies suggested that several of these bacterial species could be either human pathogens or potential pathogens. In addition, the termite gut microbiome harbors families like Lachnospiraceae and Ruminococcaceae, which have links to various gastrointestinal and extra-gastrointestinal diseases [83]. Notably, *Blautia* and *Lachnospiraceae incertae sedis*, which belong to the Lachnospiraceae, have been identified in the gut microbiome of patients with non-alcoholic fatty liver disease [84]. Additionally, it was found in a cohort

Table 1
Terrestrial invertebrates in urban and their human pathogens.

Invertebrate	Pathogen species	Pathogen	Disease	Reference
Fly	*Escherichia coli O157:H7*	Bacteria	Non-bloody diarrhea	[16]
	Toscana Virus	Virus	Febrile illnesses, neuroinvasive infections	[25]
	Norovirus	Virus	Diarrhea	[26]
	Leishmania	Parasite	Leishmaniasis	[27]
	Trypanosoma	Parasite	Trypanosomiasis	[28]
Termite	*Bacillus cereus*	Bacteria	Diarrheal-type food-borne diseases	[29]
	Brevibacillus brevis	Bacteria	Bloodstream infection	[30]
	Bacillu soleronius	Bacteria	Human rosacea	[31]
	Acinetobacter	Fungi	Blood, urinary tract, and lungs (pneumonia) infection	[32]
Cockroach	*Escherichia coli*	Bacteria	Non-bloody diarrhea	[33]
	Streptococcus Group D	Bacteria	Slow healing	[33]
	Klebsiella pneumoniae	Bacteria	Antimicrobial-resistant opportunistic infections	[33]
	Proteus vulgaris	Bacteria	Septicaemia	[33]
	SARS-CoV-2	Virus	Pneumonia	[34]
	Ascaris spp.,	Parasite	Ascariasis	[35]
	Trichuris spp.,	Parasite	Trichuriasis	[35]
	Entamoeba spp.,	Parasite	Diarrhea	[35]
	Cryptosporidium,	Parasite	Diarrhea	[35]
	Balantidium coli cysts	Parasite	Pulmonary infection	[36]
	Eggs of *Ancylostoma duodenale*	Parasite	Anemia	[36]
	Enterobius vermicularis	Parasite	Enterobiasis	[36]
	Larvae of *Strongyloides stercoralis*	Parasite	Strongyloides stercoralis	[36]
	Raillietiella hemidactyli	Parasite	Ocular infections	[37,38]
Mite	*Salmonella*	acteria	Diarrhea	[39]
	Bacillus thuringiensis	Bacteria	Diarrhea associated with food poisoning	[40]
	Aspergillus	Fungi	Invasive external otitis	[41]
	Entomophthorales	Fungi	Chronic rhinofacial disease	[42]
	Cladosporium cladosporioides	Fungi	Subcutaneous phaeohyphomycosis	[43]
	Hantavirus	Virus	Hemorrhagic fever with renal syndrome	[44]
Tick	*Ehrlichia chaffeensis*	Bacteria	Human monocytotropic ehrlichiosis	[45]
	Borrelia burgdorferi	Bacteria	Lyme borreliosis	[45]
	Francisella tularensis	Bacteria	Tularemia	[46]
	Flaviviruses	Virus	Acute encephalitis	[47]
	Nairovirus	Virus	Crimean-Congo Hemorrhagic Fever	[48]
Earthworm	*Salmonella*	Bacteria	Diarrhea	[49]
	Escherichia coli	Bacteria	Diarrhea	[24]
	Kluyvera	Bacteria	Human soft tissue infection and urinary tract infection	[50]
	Ochrobactrum	Bacteria	Septicemia	[51]
	Bacillus	Bacteria	Anthrax, local wound and eye infections and systemic diseases	[36]
Collembola	*Stenotrophomonas*	Bacteria	Respiratory infections	[23]
	Acidovorans	Bacteria	Immunocompetent infection	[52]
	Sphingomonas	acteria	Bloodstream infections and meningitis	[53]
	Methylobacterium	Bacteria	Infection in immunocompromised	[54]
	Chryseobacterium	Bacteria	Pneumonia and septicemia	[55]
	Pandoraea	Bacteria	Endocarditis and pneumonia	[56]
	Acinetobacter	Bacteria	Catheter-related infections	[57]
Snail	*Buttiauxella*	Bacteria	Surgical site infection	[58]
	Citrobacter	Bacteria	Sepsis and meningitis	[58]
	Kluyvera	Bacteria	Soft tissue and urinary tract infections	[50]
	Raoultella	Bacteria	Bacteremia	[59]
	Enterococcus	Bacteria	Resistant to common antibiotics	[60]
	Clostridium	Bacteria	Gastroenteric diseases	[27]
	Angiostrongus cantonensis	Parasite	osinophilic meningitis	[61]
	Fasciola hepatica	Parasite	Trematodiasis	[62]
	Fasciola gigantica	Parasite	Trematodiasis	[63,63]
	Angiostrongylus cantonensis	Parasite	Angiostrongyliasis cantonensis	[64]
	Alaria alata	Parasite	Schistosomiasis	[65]
Beetle	*Bacillus*	Bacteria	Periodontal disease	[40]
	Morganella	Bacteria	Sepsis, abscess, purple urine bag syndrome	[66]
	Providencia alcalifaciens	Bacteria	Diarrhea	[67]
	Proteus	Bacteria	Urinary tract infection, Crohn's disease	[68]
	Neisseria	Bacteria	Gonorrhea, meningitis and sepsis	[69]
	Serratia	Bacteria	Urinary tract infection, respiratory tract infection, meningitis	[70]
	Pseudomonas	Bacteria	Pneumonia, meningitis, pericarditis, and osteomyelitis	[71]

study that the genera Ruminococcaceae were associated with long-term insomnia, and cardiovascular metabolic diseases [85]. Acinetobacter, found in the viscera of the subterranean termite *Coptotermes heimi*, encompasses *Acinetobacter baumannii*.

Using metagenomic methods, Litov et al. [86] examined three termite species: *Hospitalitermes bicolor*, *Macrotermes carbonarius*, and *Odontotermes wallonensis*, which all exist in Cat Tien National Park in Vietnam. This study resulted in the assembly of four complete genomes of previously unknown viruses, associated with the Solemoviridae, Lispiviridae, Polycipiviridae, and Kolmioviridae families. However, the pathogenic potential of these newly discovered viruses has yet to be determined.

2.4. Cockroaches

Cockroaches are recognized as vectors for many bacterial pathogens that pose threats to human health. This study explains their role as

Table 2
Various diseases caused by terrestrial invertebrates.

Pathogens Family	Diseases	Invertebrate Hosts	Category
Bacillaceae	Diarrheal-type food-borne diseases; human rosacea; diarrhoea associated with food poisoning; periodontal disease, septicaemia, and wound infections; anthrax, local wound and eye infections; systemic diseases	Termite; Mite; Earthworm; Beetle	Bacterium
Enterobacteriaceae	Non-bloody diarrhea; hemorrhagic colitis; hemolytic-uremic syndrome; thrombotic thrombocytopenic purpura; antimicrobial-resistant opportunistic infections; septicaemia; diarrhea; human soft tissue infection; surgical site infection; sepsis; meningitis; bacteremia; urinary tract infection, Crohn's disease; respiratory tract infection, meningitis	Termite; Springtail; Mite; Earthworm; Snail; Beetle	Bacterium
Moraxellaceae	Blood, urinary tract, and lungs (pneumonia) infection; catheter-related human infections	Termite; Springtail	Bacterium
Anaplasmataceae	Human monocytotropic ehrlichiosis	Tick	Bacterium
Ancylostomatidae		Cockroach	Parasite
Ascarididae		Cockroach	Parasite
Brucellaceae	Septicemia	Earthworm	Bacterium
Burkholderiaceae	Endocarditis and pneumonia	Springtail	Bacterium
Caliciviridae	Diarrhea	Fly	Virus
Cladosporiaceae	Subcutaneous phaeohyphomycosis	Mite	Fungi
Clostridiaceae	Gastroenteric diseases	Snail	Bacterium
Comamonadaceae	Infection in immunocompetent and immunocompromised Individuals	Springtail	Bacterium
Cryptosporidiidae		Cockroach	Parasite
Diplostomatidae		Snail	Parasite
Entamoebidae		Cockroach	Parasite
Enterococcaceae	Resistant to common antibiotics	Snail	Bacterium
Entomophthorales	Chronic rhinofacial disease	Mite	Fungi
Flaviviridae	Acute encephalitis	Tick	Virus
Flavobacteriaceae	Pneumonia and septicemia in immunocompromised individuals	Springtail	Bacterium
Francisellaceae	Tularemia	Tick	Bacterium
Hantaviridae		Mite	Virus
Methylobacteriaceae	Infection in immunocompromised hosts	Springtail	Bacterium
Nairoviridae	Crimean-Congo Hemorrhagic Fever	Springtail	Virus
Neisseriaceae	Gonorrhea, meningitis and sepsis	Beetle	Bacterium
Oxyuridae		Cockroach	Parasite
Paenibacillaceae	Human bloodstream infection	Termite	Bacterium
Phenuiviridae	Febrile illnesses and neuroinvasive infections	Fly	Virus
Pseudomonadaceae	Pneumonia, meningitis, pericarditis, and osteomyelitis	Beetle	Bacterium
Psilotrichidae		Cockroach	Parasite
Raillietiellidae		Cockroach	Parasite
Schistosomatidae		Snail	Parasite
Sphingomonadaceae	Bloodstream infections	Springtail	Bacterium
Spirochaetaceae	Lyme borreliosis	Tick	Bacterium
Streptococcaceae	Slows healing during wound infection	Cockroach	Bacterium
Strongylidae		Cockroach	Parasite
Trichocomaceae	Invasive and saprophytic syndromes、invasive external otitis	Mite	Fungi
Trichurida		Cockroach	Parasite
Xanthomonadacae	Respiratory infections	Springtail	Bacterium

intermediate hosts for enteric-related parasites and enumerates the predominant bacterial, viral, and parasitic entities they harbor.

Cockroaches (*Periplaneta americana*, *Blatella germanica*, and *Blatta orientalis*) harbor a range of human bacteria, including *Escherichia coli, Group D Streptococcus*, *Klebsiella pneumoniae*, and *Proteus vulgaris* [33].

As for human pathogenic parasites, cockroaches (*Blattella germanica*, *P. americana*, *Parcoblatta* spp., *B. orientalis*, *Shelfordella lateralis*, *Periplaneta australasiae*, *Nauphoeta cinereal*) carry both nonenteric and enteric parasites, including *Ascaris* spp., *Trichuris* spp., *Entamoeba* spp., and *Cryptosporidium* spp. [35]. In addition, studies in Egypt have shown *P. americana* is a carrier of *B. coli* cysts, *A. duodenale* eggs, *E. vermicularis* eggs, and *Strongyloides stercoralis* larvae [36]. Moreover, cockroaches, particularly their larvae, can serve as intermediate hosts for parasites such as *Raillietiella hemidactyli* (Pentastomida: Raillietiellidae), reported as a zoonotic parasite that can cause human ocular infections [37,87]. Evidence from RT-qPCR assays suggests that cockroaches can act as carriers for SARS-CoV-2, with the virus being detected in both the external surfaces and gastrointestinal contents of *Blattella germanica* and *P. americana* species [34].

2.5. Mites

Mites parasitize a wide variety of metazoans, from mollusks to arthropods and vertebrates (including humans), transmitting pathogens that may result in significant health and economic repercussions [88].

Certain mites, such as poultry red mites, are known to host *Salmonella*, potentially causing diarrhea in affected individuals [39]. In addition, mites such as *Panonychus citri, Metaseiulus occidentalis*, *Phytoseiulus persimilis, Tetranychus pacificus, Tetranychus urticae*, and *Dermatophagoides pteronyssinus* are hosts for *Bacillus thuringiensis*. *B. thuringiensis*, used as an insecticide in agriculture, was previously thought to be harmless to humans. However, recent evidence suggests that the toxins it produces have been linked to a number of human infections, including food-poisoning diarrhea, gum disease, bloodstream infections, and wound infections [89].

Mites can serve as hosts for various fungi. As an example, *Dinothrombium giganteum* and *Trombidium gigas* are capable of carrying *Aspergillus* spp. Additionally, *Artoseius* spp., *Macrocheles pergrinus*, and *Pergamasus crassipes* may carry *Entomophthorales*, an entomopathogenic pathogens that have been shown to be pathogenic to humans [42]. Moreover, *Cladosporium cladosporioides* carried by *Eotetranychus* spp. may lead to subcutaneous phaeohyphomycosis in rare instances [43]. Several mite species, such as *Trombiculid*, *Gamasid*, *Leptotrombidium scutellare,* and *L. scutellare* are hosts for hantavirus [44].

2.6. Ticks

Ticks are known to transmit a multitude of pathogens. Extensive research has been devoted to examining their transmission of bacteria, particularly in tropical regions [90]. However, there are a limited number of studies investigating the consequences of fungal and parasitic diseases spread by ticks.

Ixodid ticks are capable of transmitting *Ehrlichia chaffeensis,* which is considered the most significant species responsible for causing human monocytotropic ehrlichiosis, while *E. canis* is the primary agent responsible for canine monocytotropic ehrlichiosis. Additionally, *Ixodes ricinus* complex can transmit *Borrelia burgdorferi*, the causative agent of Lyme borreliosis. *Haemaphysalis excavatum*, *Haemaphysalis marginatum*, and *Haemaphysalis parva* can harbor *B. burgdorferi* and contribute to disease in some rare clinical cases. Furthermore, it has been demonstrated that *Francisella tularensis*, a Gram-negative bacterium responsible for causing Tularemia, can be carried by various tick species, such as American dog tick (*Dermacentor variabilis*) and the lone star tick (*Amblyomma americanum*) [91].

Regarding viruses, we present an overview of recent research progress in the investigation of tick-borne flaviviruses. *Ixodes* ticks host various flaviviruses, at least seven of which have been identified as human pathogens [92]. Five of these viruses are considerable, as they cause diseases that vary from mild febrile illnesses to acute encephalitis [47]. The viruses that are responsible for Omsk Hemorrhagic Fever and Kyasanur forest disease are genetically related to the tick-borne encephalitis virus, but instead of encephalitis, they induce hemorrhagic fever [93].

2.7. Earthworms

Earthworms, such as *Eisenia andrei*, are known carriers of *Salmonella* and *E. coli*, both of which can cause health problems like diarrhea and colitis in humans [49]. A study of the gut microbiome of *Eisenia fetida* under NaCl stress revealed an increased prevalence of several pathogenic genera such as *Kluyvera*, *Lactobacillus*, and *Ochrobactrum* [24]. *Ochrobactrum*, which is phylogenetically close to *Brucella*, contains species such as *O. anthropic,* that are capable of inducing septicemia. The gut of *Pheretima guillelmi* harbors microbial communities consisting of *Bacillus, Microvirga, Blastococcus, Nocardioides,* and *Gaiella* [94]. No data are available concerning the transmission of pathogens from earthworms and to humans.

2.8. Collembolans

To the best of our knowledge, there are no clinical cases to suggest that the collembolans (springtails) transmit human bacteria, fungi, viruses, or parasites. However, some human-associated bacteria were found through our further review of the reported gut microbiome of collembolans. This section takes the two representative species, *Folsomia candida* and *Allonychiurus kimi*, as objects to shed light on any potential health risks associated with these organisms.

Ju et al. [23] investigated the effects of polyethylene microplastics on the gut microbiome of *F. candida*. Their findings revealed a significant increase in the relative prevalence of *Stenotrophomonas*, a multiresistant pathogen associated with respiratory infections [95]. In parallel, a remarkable study by Li et al. [96] revealed the presence of potential human pathogenic bacteria genera in the *F. candida* gut microbiome, including *Acinetobacter*, *Acidovorans*, *Sphingomonas*, and *Methylobacterium.*

A. kimi (Collembolan: Onychiuridae) plays a crucial role in assessing the impact of pesticides and heavy metals on soil ecosystems [97]. Upon the investigation of its gut microbiome, several bacterial genera, including *Chryseobacterium*, *Pandoraea*, *Sphingomona,* and *Acinetobacter* have been identified. Recently, there has been growing interest in the potential pathogenicity of these genera [97]. For example, *Chryseobacterium indologenes* was formerly considered a harmless microbe but is now associated with infections in immunocompromised patients, such as pneumonia and septicemia [98,55]. Furthermore, there is increasing recognition of *Pandoraea* spp. as opportunistic pathogens, with reported cases of *Pandoraea pnomenusa* causing endocarditis and *P. apista,* inducing pneumonia. In addition, *Sphingomonas koreensis* was first reported as a human meningitis pathogen in 2015 [99].

2.9. Fleas

Flea-borne infections are emerging or re-emerging worldwide, with an increasing incidence [100]. Due to fleas living in close association with humans and pet hosts (such as cats and dogs), they are of significant importance as vectors of pathogens in many parts of the world. Fleas serve as the vectors for several diseases, including plague, tungiasis, and rickettsial diseases [100]. The important vector species include *Pulex irritans*, *Ctenocephalides felsi felis*, *Ctenocephalides canis*, *Xenopsylla cheopis*, *Nosopsyllus fasciatus*, and *Echidnophaga gallinacean.* Among these, *Ctenocephalides felis felis* and *C. canis* may pose a high risk to humans due to their close relationship with pets [101,102]. Fleas and their associated zoonotic pathogens have been previously reviewed [103,104] and are not further examined here.

2.10. Snails

Snails, integral to various ecosystems and regarded as delicacies in numerous cultures, have been identified as carriers of diverse pathogens potentially detrimental to human health. These mollusks act not only as hosts but also as reservoirs, amplifying the risk of transmission of various diseases to humans upon consumption or contact.

The gut microbiome of snails harbors many human pathogenic genera. A study of two edible snails, *Helix pomatia* and *Cornu aspersum*, revealed the presence of pathogenic bacteria including *Buttiauxella*, *Citrobacter*, *Enterobacter*, *Kluyvera*, *Raoultella*, *Enterococcus,* and *Clostridium* [105]. *Enterococcus faecalis* and *Enterococcus faecium*, opportunistic pathogens, show resistance to common antibiotics [106,60]. Moreover, the terrestrial invasive giant African snail (*Achatina fulica*) has been found to harbor various biological contaminants, including *E. faecium, Staphylococcus aureus, K. pneumoniae, A. baumannii, Pseudomonas aeruginosa,* and *Enterobacter species* (ESKAPE) with drug resistance worldwide [107].

Snails serve as intermediate hosts for many human helminth parasites. For example, the giant African snail (*A. fulica*) is an intermediate host for *Angiostrongylus cantonensis*, which causes eosinophilic meningitis in humans [108]. *Radix cucunorica* also acts as an intermediate host for *Fasciola hepatica* and *Fasciola gigantica*, with the latter being transmitted to mammals [63]. Other snail-borne parasites include *Camaena cicatricosa*, which transmits *A. cantonensis,* and *Alaria alata*, a globally distributed parasite that uses snails as intermediate hosts [65]. In addition, *Biomphalaria pfeifferi* and *Bulinus globosus* are important vectors of schistosomiasis in Africa [109].

2.11. Beetles

Among Coleoptera, *Tribolium castaneum* carries *Bacillus thuringiensis,* as confirmed by Khan et al. [40], with its pathogenic properties previously established. Recent studies have concentrated on the microbial communities in the gut of Coleoptera, with particular emphasis on *Nicrophorus vespilloides*, which performs a crucial function in terrestrial ecosystems by scavenging carcasses and thus promoting the recycling of organic matter. The gut microbiome of *N. vespilloides* harbors *Morganella*, *Providencia*, *Proteus*, *Serratia*, and *Pseudomonas* during its development [110].

Similarly, *Copris incertus*, a dung beetle species, displays a varied gut microbiome comprising *Enterococcus*, *Bacteroides*, *Psycrobacter,* and *Citrobacter*. These particular bacteria have been linked to human diseases and clinical infections [111]. No data are available concerning the transmission of pathogens from beetles to humans.

3. Transmission pathways

We identify three primary pathways of human disease transmission through invertebrates based on their phenotypic and life history traits (Fig. 2): (1) direct transmission, which is defined as the host spreading pathogens on their surface through mechanical contact; (2) vector-borne transmission through invertebrate bites; and (3) transmission via contact with contaminated surfaces, feces, or urine [20,14].

3.1. Direct transmission

Invertebrate hosts commonly found in a variety of outdoor environments, such as urban parks, forests, and gardens, increase the risk of human exposure to pathogens. Leaf litter, which is abundant under park trees, provides an optimal habitat for various invertebrate taxa and serves as a nexus for breeding, hibernation, and foraging [112]. While urban forests enhance biodiversity, regulate climate, and provide recreational space, they also harbor extensive beetle communities, as observed in urban forests in New York and gardens in California [113,114]. Similarly, a study in Zurich identified 18 earthworm and 39 springtail species in 85 urban gardens [3]. Enjoying the ecosystem services of these green spaces, however, comes with inherent health risks posed by invertebrates. Urban gray areas, characterized by intensive human activity and concentration of resources, inadvertently support the survival of invertebrate hosts [115]. Underground facilities provide stable temperatures, creating an ideal environment for these hosts. The role of host biodiversity and abundance in urban areas is increasingly recognized as an important factor in human health risk studies [1].

Both adult and child populations face health risks from terrestrial invertebrates during outdoor activities. For example, children may be attracted to unique invertebrates such as giant African snails, while adults, although less likely to interact directly with invertebrates, may still be exposed through activities such as lawn mowing and gardening [116]. Reducing exposure at the source is therefore critical. Efforts should be made to restrict hosts to specific areas while promoting biodiversity, with a focus on protecting vulnerable populations such as children in settings such as nurseries, amusement parks, and pediatric hospitals. It is imperative that policymakers and stakeholders promote legislation to protect children in the context of environmental health, taking into account the vulnerability of children's immune systems and their frequent exposure to outdoor activities.

Indoor environments expose individuals to a limited range of invertebrate taxa, with some exceptions such as mosquitoes, flies, and mites. For example, Leishmania-carrying sandflies have been identified in residential areas in Brazil [117]. The distribution characteristics of cockroaches resemble those of houseflies [118]. Houseflies and cockroaches, which are predominantly found in areas characterized by inadequate sanitation, pose significant health risks to the inhabitants of these regions [119]. The implementation of environmental equity policies can, therefore, reduce the health risks faced by low-income individuals exposed to these invertebrate hosts [120].

3.2. Vector-borne transmission via bites

Ticks and fleas (*C. felis felis* and *C. canis*) possess the ability to insert their feeding mouthparts into the skin of mammals, including pets, such as dogs and cats, resulting in direct interactions [100]. As a result, these pets can inadvertently act as vectors, facilitating the transmission of tick-borne diseases to humans. In a study conducted in Poland, researchers identified a variety of human health pathogens found in ticks [121]. In particular, *I. ricinus* and *Ixodes hexagonus*, two species of clinical significance were collected from domestic dogs and cats [121]. Ticks are widespread in many urban areas, particularly those with green areas supporting tick hosts [5]. During outdoor excursions, pets frequently interact with these environments, providing opportunities for ticks to attach and potentially remain dormant in the animals. Given the close relationship and frequent physical contact between pets and their human caregivers, including behaviors such as hugging, there is a tangible risk of transmission of these vector-borne diseases, thereby posing a threat to human health. This close relationship underscores the need for vigilant surveillance and preventive measures to reduce the risk of disease transmission from pets to humans.

Flies, mosquitoes, ticks, and mites act as primary vectors in disease transmission by bites. The risk of being bitten by these vectors is heightened during prolonged outdoor activities or under conditions of poor hygiene. For instance, trombiculid and gamasid mites have been observed transmitting hantavirus to experimental mice via bites, leading to vertical transmission to offspring [44]. Given the mammalian host, a similar mechanism of bite transmission in humans cannot be ruled out.

In certain regions of Thailand, specifically Chiang Mai and Trat, there have been reports indicating that black flies have the potential to act as

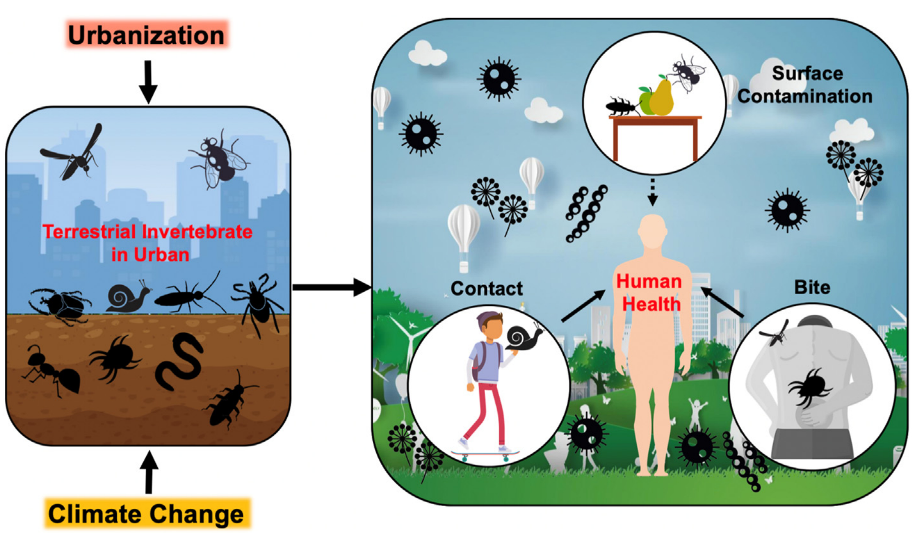

Fig. 2. The influence of urbanization and climate change on terrestrial invertebrates in urban areas and their subsequent effects on human health through three transmission pathways.

vectors for helminth parasites that affect both humans and animals. These parasites could lead to the emergence of human capillariasis, a rare disease that may be caused by bites from infected black flies [122]. Additionally, *B. burgdorferi*, which causes Lyme borreliosis, is mainly transmitted to humans via tick bites, including species such as *I. ricinus* complex, *H. excavatum*, *H. marginatum*, and *H. parva* [45]. This mode of transmission highlights the importance of preventive measures and public awareness.

3.3. Transmission via contact with feces, urine, and contaminated surfaces

The transmission of pathogens occurs through contact with invertebrate feces, urine, and surfaces contaminated with these excreta require careful consideration. It is important to note the potential of feces as a vector for *SARS-CoV-2* transmission and thus the role of invertebrates, such as cockroaches and flies, in facilitating the spread of *SARS-CoV-2* cannot be overlooked [123]. For example, significant amounts of *E. coli O157:H7*, a common cause of diarrhea and hemolytic-uremic syndrome was found in the feces of Coelopidae seaweed flies. These flies, commonly found on leisure beaches, typically feed on decaying seaweed and, as such, can serve as vectors for *E. coli O157:H7*, potentially endangering individuals.

Sandflies are known to transmit Leishmania parasites to humans, mainly through bites. However, recent studies have revealed the presence of Leishmania in their gut microbiome [81]. This discovery suggests the possibility of the transmission of *Leishmania* through sandfly feces, thereby adding to the range of illnesses identified as leishmaniasis. Sandflies, which are often found indoors during warmer seasons, can deposit their gut microbiomes—along with associated pathogens—on different surfaces, including desktops, food, and household items, during excretion. This contamination heightens the risk of pathogen transmission to humans, as identified by the detection of fly feces in food preparation areas in Maputo, Mozambique, increases the risk of both foodborne and contact infections [20]. The findings suggest a need for improved sanitation practices to reduce exposure to contaminated surfaces. Implementing strict hygiene practices can reduce the possibility of infections arising from consuming food contaminated by fly feces [20]. It is important to note that, unlike mechanical transmission, pathogens are found in feces and urine can endure in an environment for prolonged periods of time [124]. Therefore, individuals may face exposure to these pathogens even in environments that seemingly lack invertebrates. The scant quantity of excreta produced by invertebrates, which is often imperceptible without magnification, adds a layer of complexity to attempts to prevent contamination. This highlights the imperative of maintaining vigilance and taking the necessary precautions, such as sanitizing surfaces before food preparation.

4. Impact of urbanization on invertebrate-associated human pathogens

Urbanization has heterogeneous effects on human pathogens carried by invertebrates [125]. Urbanization influences invertebrate phenotypes from an internal perspective and alters their living condition from an environmental perspective. These changes are driven by the degradation of ecological environments, increased population density, an influx of building materials, and the urban heat island effect. Consequently, urbanization modifies the interactions between hosts and landscapes, thereby altering the risk of zoonotic diseases.

4.1. Urbanization enhances the health risks of invertebrates via different aspects

Urbanization may increase the risk of transmission for invertebrate-associated human pathogens. Research tracking Chagas disease transmission through insects in Peru showed that *T. cruzi* transmission predominantly occurred in highly urbanized communities [126]. The influx of building materials, people, and animals can create conditions that enhance the spread of vector-borne diseases. On the other hand, urban waste, a key source of nutrition and contamination, contributes to the development of some invertebrate communities, such as flies and cockroaches [127].

Changes in land use due to urbanization can intensify the risk of infection through various mechanisms, such as increased host abundance, higher exposure frequency, and faster disease development. Soil properties, urbanization, and landscape layout can influence earthworm community distribution. Additionally, the age of residential structures has a noticeable impact on earthworm abundance [128]. Rapid urbanization and population growth intensify interactions between sandflies and humans on city outskirts, which harbor diverse species compositions, including a higher number of seasonal sandfly species. For instance, species like *Evandromyia evandroi* and *Brumptomyia avellari* complicate leishmaniasis transmission [129].

Furthermore, urbanization can promote the growth and maturation of specific vector species, potentially introducing diseases to regions previously unaffected. While schistosomiasis was once believed to be exclusive to rural areas, recent reports suggest its presence in suburban and urban areas, indicating its expansion [109]. Urbanization might also enlarge the habitats suitable for *Aedes* larvae, hasten their growth, and increase their survival rate, possibly elevating the prevalence of mosquito-borne diseases in densely populated zones [130].

Land-use alterations, especially the extent of urban greening, can impact human infections. Urban greening seems to modify the survival range of small rodents that support tick populations [131], subsequently influencing the occurrence of clinical-significant tick genera like *Amblyomma*, *Haemaphysalis*, and *Ixodes*. This suggests that more extensive urban greening might elevate tick-borne disease risks [131]. Land-use shifts during urbanization could impact food webs and result in the spillover of emerging infectious diseases [132]. Fly and mosquito larvae primarily consume bacteria, protozoa, nematodes, diatoms, algae, and organic waste in their habitats. Such land-use transformations might influence the growth rate of these host populations within the food web [133].

4.2. Urban warming and the escalation of vector-borne disease risks

Global warming is one of the most urgent problems in the anthropocene [134]. Global warming is manifested as an urban heat island effect in urban areas. Here we explore the scenarios for the urbanization-warming interface. Urban warming has the potential to alter phenotypic traits of hosts, leading to changes in vector-borne disease transmission rates influenced by metabolism, extrinsic incubation period, and transmission rate [135]. Changes in host phenotypes are likely to facilitate the expansion of many vector-borne diseases, as observed in previous studies [129]. Moreover, global warming can enhance the metabolism of poikilothermic animals, including invertebrates. The reproductive and survival rates of the invertebrates are elevated, which consequently increases their population [136]. Warming climate conditions have been shown to extend the activity periods of invertebrates, notably ticks and mosquitoes, as detailed in Nabbout et al. [137]. This phenomenon, including increased tick activity during warmer winters, leads to longer active seasons and may heighten human-invertebrate contact, presenting emerging public health concerns [137].

4.2.1. Vectors or hosts spread to more areas

A previous study indicated that, under the effects of climate warming, the duration of malaria transmission could extend from five to six months annually between 2051 and 2080, compared to the baseline period of 1991–2007 [138]. As a result, regions such as southern and southeastern Europe may witness an uptick in vector stability and receptivity, owing to increased temperature suitability for hosts [139,140]. Nevertheless, it is crucial to note that these are predictions, and the actual trends remain unresolved. Historically, the eradication of mosquito-borne diseases in Europe were more closely linked with socioeconomic advancements than solely environmental factors [141].

On a broader scale, rising global temperatures may facilitate the influx of tropical or subtropical diseases into mid-latitude regions. The extrinsic incubation period of the Zika virus in mosquito hosts could be shortened by climate warming, thereby facilitating its transmission [142]. Such elevated temperatures have been observed to bolster the capacity of *A. albopictus* to transmit the Zika virus, consequently expanding the scope of mosquito-borne diseases to previously unaffected mid-latitude regions [140]. The alterations in mosquito-borne disease patterns are exemplars of a wider trend. Climatic warming is anticipated to transform the formerly unsuitable cold areas into habitable locations for multiple invertebrate hosts, including ticks. Forecasts reveal the potential for the doubling of tick-friendly habitats in Canada and a significant expansion in southern Europe by 2080 [129]. Such variations in the surroundings may pave the way for a surge in tick-borne illnesses in these regions.

A comparable pattern has been observed in specific species of snails *B. globosus*, which serves as an intermediary host for *Schistosoma haematobium*, and is impacted by external temperatures because it cannot regulate its body temperature [143]. Over the last 30 years, the average January temperature in China has increased by 1 °C due to a century of global warming. As a result, it is assumed that the potential distribution boundary of *B. globosus* has shifted northward, which could potentially invade China's mainland and lead to an expansion of *S. haematobium*. Furthermore, other snails that are thermally tolerant may also experience an expansion of their habitat ranges due to global warming [143]. For example, *Echinolittorina* can thrive in temperatures as high as 55 °C and, as a result of global warming, may be able to expand its range to mid-high latitudes [144]. Given that many snails serve as disease vectors [116], an increase in temperature is projected to expand the areas where these diseases are prevalent.

What the expansion trend affects in urban areas still lacks large-scale research, but some research is constructive and insightful. The invasive African giant snails (*A. fulica*) have been considered emerging hazard organisms in urban and harbor significant health risks. Furthermore, urbanization increases risks, as relative abundance of human pathogens in the gut microbiome if urban snails is significantly higher than in suburban or rural [116]. Urbanization may alter the ecological niche of existing diseases by introducing invasive species [145,146]. The increase in alien species due to urbanization has been documented in many areas, highlighted by the emergence of ticks from the *Argas reflexus* group and *Rhipicephalus sanguineus sensu lato* in urban areas [147].

4.2.2. Indirect impact on critical public facilities

Urban warming could lead to a rise in the frequency and intensity of extreme weather events, such as heavy rains and tropical storms. This may indirectly impact vital public amenities. Furthermore, such climate changes can affect the spread of vectors, thereby increasing the number of infectious diseases [96]. For example, Daniel et al. [148] found a correlation between the spread of tick-borne encephalitis and extreme weather conditions, including flooding and abnormally high temperatures.

The effective operation of drainage systems is a crucial strategy for controlling vector-borne diseases, especially those transmitted by ticks and mosquitoes [149]. In Europe, the occurrence of mosquito-borne diseases such as West Nile virus and malaria has declined, partly due to extensive land drainage projects from the past [150]. However, extreme rainfall events, which are becoming more frequent due to climate change, have the potential to compromise the effectiveness of urban drainage systems. This can result in urban flooding, causing stagnant water to accumulate on streets and sewage to backflow. These conditions provide a suitable environment for the breeding of invertebrates hosts, such as mosquitoes and flies, which in turn elevate the risk of transmitting diseases to humans [149]. The current state of affairs requires the improvement and adaptation of public healthcare facilities and infrastructure to effectively mitigate the hazards associated with the changing climate and safeguard public health.

5. Discussion

5.1. Integrated management approaches for urban invertebrates

To effectively address the challenges posed by urban invertebrates, a multifaceted strategy is essential. This strategy encompasses the application of biological and ecological control methods, which have demonstrated efficacy in diverse ecosystems. The widespread use of insecticides, while common, face limitations due to health risks to humans and the development of drug resistance in host species [151]. Efforts to eradicate ticks have often been unsuccessful due to the emergence of acaricide resistance [152].

In recent years, the use of biological control methods in managing urban invertebrates has garnered increasing attention. The life stages of these invertebrates, influenced by their exposure to different habitats, occupy unique ecological niches. Utilizing natural predators for intervention is particularly promising in this context. For example, controlling mosquito populations through deploying tadpoles, which prey on mosquito larvae, has proven effective [153]. Additionally, the application of gene-modified organisms in mosquito control represents an innovative approach. Yet, the deployment of such methods necessitates careful consideration of their legal and ethical implications [154].

It is important to note, however, that strategies focusing primarily on extermination are suitable for only a limited range of taxa, specifically those like mosquitoes, flies, and ticks, which are directly addressed in our study. Achieving a harmonious balance within socio-economic-ecological frameworks are essential for the management of most taxa. The role of invertebrate hosts in maintaining ecological balance, although not fully defined quantitatively, is underscored by the "dilution effect". This concept emphasizes the significance of preserving biodiversity as a means to mitigate the health risks associated with vector-borne diseases [1]. Our overarching aim is to establish a consistent approach that integrates ecological considerations with public health perspectives.

5.2. Enhancing pathogen surveillance and control

Effective surveillance of pathogens within urban ecosystems is essential for public health safety. The application of molecular and bioinformatics tools significantly enhance our capabilities for early detection and identification of potential pathogens carried by invertebrates. Pathogen databases have emerged as powerful tools for early monitoring. The Molecular Based Pathogen Database (MBPD) presents a comprehensive resource supporting "one-health" practices [10]. Similarly, ZOVER, a virus database with a focus on invertebrate vectors, offers crucial information for pathogen tracking [12]. Given the increasing prevalence of emerging infectious diseases, the ongoing updating and maintenance of such databases is critical.

However, the process of pathogen monitoring is not without its legal challenges, particularly when it involves accessing private properties. A promising solution to this obstacle is citizen science. This approach actively involves the public in scientific research as both data collectors and analyzers, thereby circumventing certain legal limitations. For example, a citizen science yielded valuable data on termite distributions [155]. The rise of citizen science as a methodology is proving indispensable in gathering extensive data within legal frameworks, enhancing our understanding of pathogen dynamics in urban settings [156].

5.3. Strengthening urban planning and public health policies

Urban planning is crucial in mitigating the spread of diseases transmitted by invertebrates [157]. The strategic development of green spaces, effective water management systems, and infrastructure that inhibit vector breeding and proliferation are vital. Green spaces not only enhance urban biodiversity but also contribute to the "dilution effect", where increased biodiversity results in a lower risk of human disease due to the prevalence of less competent hosts [1]. We advocate for the adoption of an Urban One Health approach, which integrates the management of urban systems with effective control of zoonotic diseases [158]. Implementing policies and practices that integrate public health considerations into urban design is paramount in reducing the risks associated with urban invertebrates [20].

5.4. Collaborative efforts in urban ecosystem health

Urbanization presents a paradox in disease ecology, balancing between urban health challenges and benefits for individual and community health outcomes. The dynamics of zoonotic diseases, including those that are vector-borne, within urban social-ecological systems are shaped by intricate interactions among human and environmental factors [158]. Addressing the multifaceted challenges presented by urban invertebrates require collaboration among ecologists, urban planners, public health officials, and community members [159]. Public education and engagement initiatives are essential in raising awareness about urban ecosystem health and the significant roles individuals can play in risk mitigation.

6. Conclusion

This comprehensive review synthesizes the human pathogens associated with significant terrestrial invertebrate species in urban environments. We elucidate how these pathogens threaten the health of urban populations through established pathways. Our focus then shifts to the potential effects of pressing global issues. We examine the impacts of urbanization on invertebrate hosts, vectors, and associated human pathogens, providing insights into the dynamic relationship between these factors. Our review then emphasizes the complex trade-offs inherent in urban development, highlighting the essential need for careful management of these trade-offs. Addressing these challenges necessitates cross-sectoral collaboration and active stakeholder engagement, aiming to develop policies that effectively integrate health and environmental considerations. We have identified numerous areas where further evidence is needed to optimize the management of urban ecosystems, considering both ecological integrity and human health risks. Our review aims to serve as a valuable reference for ecologists, public health experts, city planners, and policymakers, providing fundamental knowledge to guide future research, policy development, and public health interventions.

CRediT authorship contribution statement

X.S.: conceptualization, project administration, resources, supervision, visualization, writing–review & editing. A.X.: conceptualization, data curation, writing–original draft. Y.Y.Z.: conceptualization, visualization, writing–original draft, writing–review & editing. M.B., X.L.A., Q.S.H., J.Q.S.: writing–review & editing. H.F.Y.: visualization.

Declaration of competing interests

The authors declare no competing financial interest.

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