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Review

Global spillover of land-derived microbes to Ocean hosts: Sources, transmission pathways, and one health threats

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ABSTRACT

Terrestrial pathogens are increasingly being detected in marine organisms, raising concerns about ecosystem sustainability, biodiversity loss, and threats to human health. Over the past two decades, reports of microbial contaminants crossing from land to sea have increased, suggesting shifts in pathogen ecology driven by environmental changes and human activities. Pathogens originating on land can spread, adapt, and persist in marine environments, infecting a wide range of hosts and potentially re-entering terrestrial environments. Despite growing recognition of this issue, a comprehensive understanding of the distribution, diversity, and transmission pathways of these pathogens in marine ecosystems remains limited. In this Review, we provide a global analysis of terrestrial pathogen contamination in marine animal populations. Drawing from pathogen detection data across 66 countries, we used phylogenetic methods to infer land-to-sea transmission routes. We identified 179 terrestrial pathogen species, including 38 bacterial, 39 viral, 80 parasitic, and 22 fungal species, in 20 marine host species. Terrestrial pathogens are not only widespread but also highly diverse in marine ecosystems, highlighting the frequency and ecological significance of cross-system microbial exchange. By revealing the scale and complexity of land-to-sea pathogen flow, we show that climate change, pollution, and other anthropogenic pressures may intensify pathogen spillover events, with potential feedback effects on terrestrial systems. This highlights the urgent need for integrated surveillance and policy frameworks acknowledging the interconnectedness of terrestrial and marine health. Our work advocates a One Health approach to microbial ecology, stressing the need to safeguard marine and human populations from emerging cross-system threats.

1. Introduction

The contamination of marine waters by terrestrial pathogens is an increasing concern, given the ocean's vital role in sustaining human societies—particularly through food production and climate regulation [1–4]. Terrestrial pathogens, including bacteria, fungi, viruses, and parasites, originate in land-based ecosystems and rely on specific hosts—such as animals, plants, or humans—for reproduction and transmission. In contrast, aquatic pathogens are adapted to survive and spread within water-based environments. Interestingly, some microorganisms, referred to as amphipathic pathogens, can persist in both terrestrial and marine ecosystems. Examples include *Vibrio* species (e.g., *V. vulnificus*), *Brucella* species, and enteric bacteria such as *Salmonella* and *Escherichia coli*. Although primarily terrestrial, these pathogens exhibit a remarkable ability to survive, disseminate, and cause disease in marine environments by adapting to varying physicochemical conditions [3–5]. Their persistence in seawater enables them to integrate into marine food webs, posing emerging threats

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to both ecosystem integrity and human health.

The presence of terrestrial pathogens in marine ecosystems represents a growing public health risk [6,7]. These pathogens can adhere to surfaces such as phytoplankton and microplastics, enhancing their survival and promoting wide dispersal in seawater [8–12]. Contaminated filter-feeding mollusks can further introduce them into the food chain, increasing the incidence of foodborne illnesses in humans, including gastrointestinal disorders like diarrhea and vomiting [13,14]. As such, their presence in edible marine organisms has become a significant global concern for food safety and public health [15].

Despite the ocean's rich and dynamic biodiversity, it is increasingly threatened by the influx of terrestrial pathogens [16,17]. These microorganisms reach marine environments via various anthropogenic and natural pathways, including maritime transport, aquaculture, coastal development, extreme weather events, and wildlife migration [18–20]. Climate variability further exacerbates their spread and persistence, undermining the ecological balance of marine ecosystems [21]. Understanding these transmission routes is essential to assess the broader ecological impacts of terrestrial pathogen contamination.

While research into land-to-sea pathogen transmission is expanding, the taxonomic and phylogenetic relationships of many terrestrial pathogens remain poorly characterized. This limitation hampers our ability to trace their origins and understand their transmission dynamics. In this review, we provide a comprehensive analysis of the distribution of terrestrial pathogens identified in marine organisms, using taxonomic and phylogenetic frameworks to explore their origins. We also examine the mechanisms by which these pathogens infiltrate marine ecosystems and assess their potential impacts on marine biodiversity and human health. Finally, we highlight critical knowledge gaps and emphasize the urgent need for targeted research to mitigate the increasing threat these pathogens pose to ocean health and human well-being.

2. Methods

2.1. Literature search strategy and article selection

This review is based on a comprehensive literature search conducted across five major bibliographic databases: Web of Science, PubMed, ScienceDirect, China National Knowledge Infrastructure (CNKI), and Wanfang Data, focusing on English-language articles published up to December 31, 2023. To ensure thorough coverage, we also manually reviewed the bibliographies of relevant articles. The search strategy employed a broad range of keywords relating to marine host organisms, including “marine animal,” “marine mammal,” “marine reptile,” “marine bird,” “marine arthropod,” “marine mollusc,” “marine coelenterate,” “marine sponge,” “marine protozoa,” “marine annelid,” and “marine echinoderm.” In addition, we used pathogen-related terms such as “pathogen,” “bacteria,” “virus,” “parasite,” “fungus,” and “microorganism.” Scientific and common names of terrestrial pathogens known to infect marine hosts were also incorporated into the search strategy.

The initial search yielded a total of 1756 bibliographic records. After removing duplicates using EndNote X9, 1342 unique records were retained for screening. Two independent reviewers (H.-C. Song and T. Yang) screened the titles and abstracts of these records. Of the 1342 studies, 414 were excluded based on predefined inclusion and exclusion criteria. To be included, studies had to meet the following conditions: (i) provide valid and original data, (ii) focus on the detection of terrestrial pathogens in marine organisms, (iii) clearly define the terrestrial origin of the pathogen, (iv) report data derived from wild rather than captive animals, and (v) be published as full-text research articles, excluding reports, reviews, conference abstracts, and other non-peer-reviewed literature. The selected studies were used to compile a list of marine host species and the various terrestrial pathogens identified in them, as detailed in Supplementary Table S1. Data were extracted from the included studies and analyzed using the R programming language for visualization and interpretation.

2.2. Pathogen classification and selection criteria

A major challenge in this study was classifying pathogens as terrestrial or aquatic, particularly in cases involving generalist pathogens capable of infecting both host types. Some pathogens associated with terrestrial animals may be well adapted to aquatic environments, while others that primarily inhabit terrestrial ecosystems can opportunistically infect marine species. To address this complexity, we classified pathogens based on their predominant habitat, primary transmission medium, and ecological and epidemiological characteristics reported in the literature. For example, although some *Vibrio* species (e.g., *V. vulnificus*) can infect terrestrial animals, they were classified as aquatic pathogens in this study due to their primary association with marine or brackish environments and their reliance on water for survival, reproduction, and transmission [22].

To ensure accurate classification, we conducted an in-depth review of the scientific literature, prioritizing studies that documented the presence of pathogens in both terrestrial and marine hosts. Emphasis was placed on reports that included genetic sequence data accessible in public repositories. In cases where ambiguity remained, pathogens were categorized according to widely accepted scientific classifications to maintain consistency while acknowledging the ecological complexity of generalist species. Additionally, we retrieved genetic sequence data from GenBank and other publicly available databases using accession numbers and keyword searches, incorporating terms such as pathogen names, host species, and environmental sources. This integrative approach allowed us to build a robust framework for understanding how pathogens move between terrestrial and aquatic ecosystems and to highlight the taxonomic and ecological overlaps that complicate their classification.

2.3. Phylogenetic analysis

Representative sequences of selected bacterial, viral, and parasitic pathogens were obtained from studies that met the inclusion criteria. These included 16S ribosomal RNA (16S rRNA) gene sequences for *Brucella* spp. (Supplementary Table S2), nucleocapsid protein sequences of morbilliviruses (Supplementary Table S3), and 18S ribosomal RNA sequences for *Sarcocystis* spp. (Supplementary Table S4). All sequences were aligned using default parameters in MEGA7 (v7.0.26). Phylogenetic trees were constructed using the maximum likelihood method implemented in RAxML (v0.9.0), with 1000 bootstrap replicates to assess the robustness of the tree topology. The resulting trees were visualized and annotated using the Interactive Tree of Life (iTOL) tool.

3. Global distribution and seasonal fluctuation

3.1. Frequency and distribution of terrestrial pathogens in marine environments

Among the terrestrial pathogens identified in marine environments, bacteria were the most frequently reported group, while parasites exhibited the greatest species diversity. A total of 38 species of terrestrial bacteria have been detected in marine fauna [17–21], with most cases reported along the eastern and western coasts of North America, Western Europe, Oceania, and Japan. Occasional occurrences were also recorded in South America and Antarctica (Supplementary Fig. S1a). A small subset of *Mycoplasma* and *Chlamydia* species, typically transmitted by blood-feeding arthropods such as ticks and mosquitoes, accounted for fewer than 3 % of reported cases [22]. Terrestrially derived viruses have been identified along the eastern and western seaboards of the United States, the southeastern coast of South America, the coasts of Western Europe and the Mediterranean, the eastern coast of China, and in Oceania (Supplementary Fig. S1b).

Parasites represented the most species-rich group, with approximately 80 species reported in marine environments. These cases were primarily concentrated in North and South America, Western Europe, and Oceania, with additional records from Asia—particularly Japan—and Antarctica (Supplementary Fig. S1c). Fungal transmission from land to sea was mainly documented in the United States, Japan, and various Western European countries (Supplementary Fig. S1d). Overall, most studies on the transmission of terrestrial pathogens to marine ecosystems have been conducted in economically developed regions. In contrast, there is a lack of epidemiological data from low- and middle-income countries, likely reflecting disparities in research funding, surveillance capacity, and public health infrastructure.

Addressing the transmission of land-based pathogens to marine environments requires a multidisciplinary approach that integrates environmental science, public health, ecological monitoring, and international collaboration. Key strategies include improving environmental surveillance, upgrading water treatment and wastewater infrastructure, strengthening public health systems and emergency response capacities, promoting cross-sector and international partnerships, and restoring natural ecosystems. Furthermore, raising public awareness, developing predictive disease models and early warning systems, and establishing a comprehensive prevention and control framework are essential to mitigating the transfer of pathogens between terrestrial and marine ecosystems—ultimately safeguarding both public health and environmental integrity.

3.2. Seasonal variation

The occurrence of terrestrial pathogens in marine animals tends to peak during the summer months or the subsequent rainy season. This post-summer period, typically occurring before autumn, is characterized by heavy precipitation and high humidity. Depending on local climatic conditions, it may persist for several weeks to months [23–25]. This seasonal pattern is well documented: elevated temperatures during summer promote pathogen growth and proliferation, while increased rainfall enhances surface runoff, facilitating the transport of terrestrial pathogens into marine ecosystems [26]. Our analysis also highlights regional differences in pathogen frequency, particularly in coastal areas of several countries. In Western Europe, specifically in the United Kingdom, Spain, Italy, Norway, France, and Germany, a humid oceanic climate with year-round temperatures remaining above 0 °C creates persistent environmental conditions conducive to the survival and transmission of terrestrial bacteria [27,28].

4. Risk factors

4.1. Environmental factors

Several environmental factors can increase the risk of pathogen transmission, thereby increasing the susceptibility of marine organisms to infection. Climatic and weather events, such as flooding and strong winds, can facilitate the introduction of terrestrial pathogens into marine ecosystems [26,29,30]. For example, climate change-driven flooding in Italy has been associated with the contamination of coastal waters by pathogens including *Salmonella*, *E. coli*, *Listeria monocytogenes*, *Toxoplasma gondii*, Hepatitis A virus, and severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) [31]. Other environmental features, such as river and coastal topography, including tides, currents, and estuarine wave activity, also influence the spread of terrestrial pathogens into marine environments [32]. Additionally, ecosystem degradation and reduced biodiversity among potential host species (e.g., birds, rodents, and amphibians) can further facilitate pathogen dissemination [33,34]. Chronic exposure to environmental pollutants, such as heavy metals, may exacerbate infections in marine mammals by impairing immune function and increasing susceptibility to terrestrial pathogens [35]. Coinfections involving multiple pathogens can further intensify disease severity, as immunosuppression in the host allows other pathogens to establish and proliferate [36,37].

4.2. Anthropogenic factors

Human activities significantly contribute to the introduction and spread of terrestrial pathogens in marine environments. Anthropogenic pollutants, including industrial effluents, untreated municipal sewage, and agricultural runoff, often carry a broad spectrum of pathogens. The direct discharge of untreated waste into coastal waters serves as a major route for the entry of land-derived pathogens into the sea [38–41]. Hydrological and atmospheric forces, such as water currents and air movements, can facilitate both direct and indirect transport of these pathogens over large distances [42,43]. For example, surface runoff is a key mechanism for transmitting *T. gondii* oocysts into marine systems [44]. Moreover, under favorable climatic conditions, bacteria and fungi can become aerosolized and transported into marine environments via the atmosphere [45–48]. Other anthropogenic activities, including coastal development, tourism, pollution, and overfishing, further increase the risk of pathogen introduction, as summarized in Box 1.

4.3. Marine ecosystem

Once terrestrial pathogens enter the ocean, they exploit various marine habitats and develop strategies to survive in dynamic conditions. Many of these pathogens associate with phytoplankton and zooplankton, the base of marine food webs, which inadvertently facilitate pathogen persistence and dispersal [49,50]. Zooplankton, in particular, may act as carriers of land-derived pathogens, with water currents and wind aiding their spread [51]. However, it remains uncertain whether these pathogens have adapted specifically to planktonic life or if plankton merely serve as passive vectors. Due to their ecological ubiquity and exposure to diverse environments, plankton may play a critical role in transporting a wide range of pathogens throughout marine systems [52]. In addition, worms, molluscs, and their eggs and juveniles can act as vectors for terrestrial pathogens, particularly following runoff or flooding events [53,54].

Plankton provide nutrient-rich and protective microenvironments that can support the survival, reproduction, and transmission of terrestrial pathogens such as *Vibrio cholerae*, *Salmonella*, *E. coli*, *T. gondii*, Hepatitis A virus, Rotavirus, and *L. monocytogenes* [55,56]. Plankton also engage in horizontal and vertical migration, enabling the spread of associated pathogens across multiple oceanic zones and expanding their ecological reach [17,57]. To

Box 1
Anthropogenic factors contributing to the spread of terrestrial pathogens in marine environments.

- ***Intensive aquaculture.*** Intensive aquaculture, particularly operations that rely on feed supplements—can contribute to water pollution and facilitate the spread of pathogens within marine environments [62]. Pathogens introduced into aquaculture systems may be disseminated via intermediate hosts, water currents, and substrates, potentially affecting surrounding ecosystems [63]. Coastal mariculture is especially significant in facilitating the transmission of terrestrial pathogens into the sea. Pollution associated with aquaculture, including industrial waste, microplastics, and nutrient-driven algal blooms, can alter the composition of bacterial communities in aquaculture waters. For instance, the detection of *Halomonas* and *Sulfitobacter* in heavily polluted areas of the Thermaikos Gulf in northern Greece suggests that anthropogenic pollution may be selecting for bacteria adapted to contaminated environments. Moreover, the presence of *Planococcus*, a genus linked to plastic debris, indicates a potential vector for microbial transport—potentially including terrestrial pathogens [64].
- ***Overfishing.*** Excessive fishing can lead to the decline of key marine species, reduce biodiversity, and disrupt ecological balance. These changes may weaken ecosystem resilience and create conditions favorable to pathogen persistence. Additionally, fishing equipment and harvested organisms can act as physical vectors, aiding in the spread of terrestrial pathogens into marine systems [65].
- ***Riverine and coastal development.*** Infrastructure projects such as hydroelectric dams, dikes, and land reclamation can significantly alter riverine and coastal hydrology, leading to changes in water flow and ecosystem structure. These developments may degrade water quality and disturb natural habitats, increasing the vulnerability of marine environments to the introduction and persistence of land-derived pathogens [66].
- ***Marine tourism.*** Marine tourism**,** including recreational water activities and the discharge of untreated human waste, can introduce human pathogens directly into marine ecosystems [67]. Such contamination heightens the risk of introducing terrestrial pathogens into the ocean, posing threats to both marine biodiversity and public health.

enhance their resilience in marine conditions, terrestrial pathogens may form spores or secrete microvesicles, aiding their survival on or within zooplankton hosts [58,59]. Given that plankton constitute the foundational food source for a wide array of marine organisms [60], they can facilitate the upward transmission of terrestrial pathogens through the food web. For example, planktonic vectors have been implicated in the transmission of *Vibrio aestuarianus* 02/041 to Pacific oysters (*Crassostrea gigas*) [61].

5. Types of terrestrial pathogens and their marine hosts

5.1. Bacteria

A wide array of bacteria has crossed from terrestrial environments into marine ecosystems, with 38 genera identified in marine organisms [68–72]. Among these, *Brucella* spp.—including several subspecies—are the most frequently reported, with over 100 documented cases. Other commonly detected bacteria include *Vibrio* spp., *Streptococcus* spp., *Mycobacterium* spp., *Helicobacter pylori*, *L. monocytogenes*, *Salmonella* spp., *Klebsiella pneumoniae*, *E. coli*, and *Campylobacter* spp. (Fig. 1a). While some *Mycobacterium* species are naturally associated with aquatic environments [73], the majority are terrestrial in origin, commonly found in animals, soil, and air. These bacteria typically do not rely on aquatic environments for survival or transmission, which often occurs via air or direct contact. As such, *Mycobacterium* spp. are categorized in this review as a major group of terrestrial pathogens.

The World Health Organization's Expert Committee on Brucellosis recognizes six *Brucella* species and 19 subtypes, many of which are specific to terrestrial animals such as sheep, cattle, and swine [74]. More recently, species such as *Brucella ceti*, *B. pinnipedialis*, *B. inopinata*, *B. papoonis*, and *B. vulpis* have been identified in marine hosts, including cetaceans (whales, dolphins), pinnipeds (seals, sea lions, walruses), sea otters, and other marine species like fish, shellfish, sea turtles, and seabirds [75]. These marine *Brucella* strains share high genetic similarity with their terrestrial counterparts. Intriguingly, *Brucella* has also been found in marine plants and amphibians, suggesting a broader ecological distribution than previously understood [76,77].

5.2. Viruses

To date, 39 terrestrial-origin viruses have been detected in marine organisms. Among the most frequently reported are morbilliviruses, herpesviruses, influenza A virus, SARS-CoV-2, hepatitis E virus, papillomaviruses, poxviruses, adenoviruses, alphaviruses, and caliciviruses (Fig. 1b). Morbilliviruses, with over 100 recorded infections in marine animals, belong to the *Paramyxoviridae* family. These enveloped viruses possess a single-stranded, non-segmented, negative-sense RNA genome [78]. Seven morbillivirus species are recognized: measles virus (MV), canine distemper virus (CDV), rinderpest virus (RPV), peste des petits ruminants virus, cetacean morbillivirus (CeMV), phocine distemper virus (PDV), and feline morbillivirus (FeMV). Among these, CDV, CeMV, and PDV are most commonly identified in marine mammals such as seals, whales, dolphins, and sea lions. Although CeMV and PDV primarily circulate within marine mammal populations, they are closely related to terrestrial viruses such as CDV and MV. Infected marine animals often develop severe illness or immunosuppression, predisposing them to secondary infections [79].

5.3. Parasites

Parasites represent the most commonly reported land-to-sea-transmitted pathogens, with at least 80 species identified in marine hosts (Fig. 1c). These include protozoans such as *T. gondii*, *Sarcocystis* spp., *Cryptosporidium* spp., and *Giardia duodenalis*, as well as nematodes like *Anisakis* spp., *Uncinaria sanguinis*, *Perkinsus mediterraneus*, *Contracaecum osculatum*, and *Pseudoterranova decipiens*. *T. gondii* is particularly significant due to its complex life cycle, involving felids as definitive hosts and a broad range of intermediate hosts [80]. Although traditionally considered a terrestrial parasite, increasing evidence highlights its impact on marine ecosystems. *T. gondii* oocysts are highly resilient, enabling them to persist in harsh oceanic environments [81–83].

Recent global genotyping studies have revealed far more genetic diversity in *T. gondii* than previously recognized. While

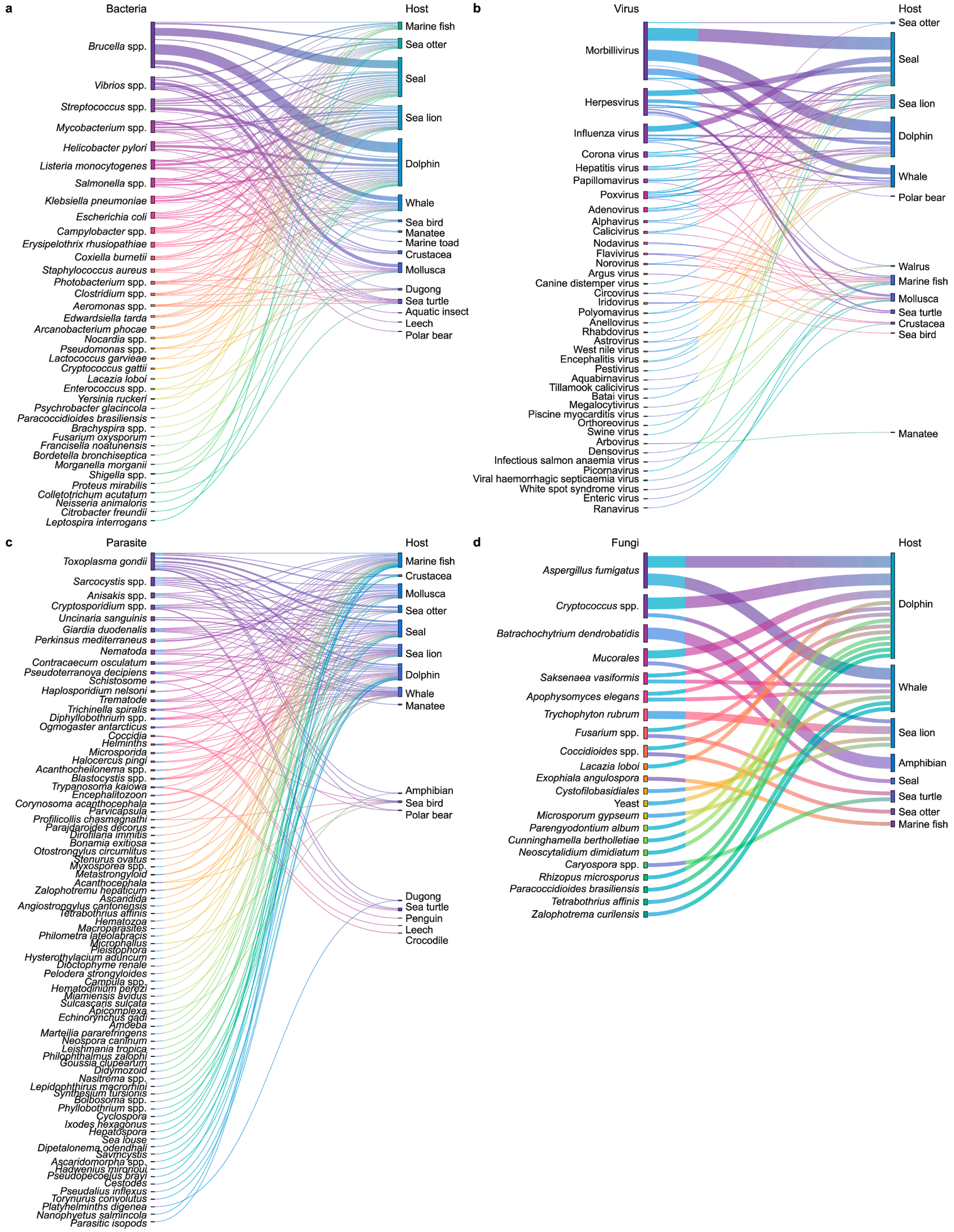


Fig. 1. Taxonomic association between terrestrial pathogens and their marine hosts. This global classification illustrates the transmission of terrestrial pathogens from land to marine environments. Marine hosts of terrestrial bacteria (**a**), viruses (**b**), parasites (**c**), and fungi (**d**) are documented based on 414, 360, 293, and 39 epidemiological reports, respectively. Colors represent distinct pathogen species, while connecting lines represent known host-pathogen associations. Detailed information on pathogen types and their corresponding hosts is available in Supplementary Table S1.

earlier classifications focused on clonal types I, II, and III [84,85], newer findings indicate the prevalence of recombinant and atypical genotypes in both terrestrial and marine systems [86,87]. This diversity points to complex environmental transmission pathways [88].

Marine species may serve as either mechanical vectors, such as filter-feeding invertebrates like bivalves, or intermediate hosts, including marine mammals such as sea otters, dolphins, and seals [89,90]. Invertebrates aid in passive transport of oocysts, whereas mammals typically acquire infection through ingestion of contaminated prey or water [91]. Land-to-sea transmission of *T. gondii* is primarily associated with freshwater runoff contaminated by felid feces [21]. This growing body of evidence underscores the need for an integrated research approach. Future investigations should combine genomic surveillance, environmental monitoring, and marine wildlife health assessments to better understand *T. gondii* ecology in marine ecosystems [92].

5.4. Fungi

Fungal pathogens are less commonly reported in marine organisms compared to bacteria, viruses, and parasites. Nonetheless, several species, including *Aspergillus fumigatus*, *Cryptococcus gattii*, *Cryptococcus albidus*, *Batrachochytrium dendrobatidis*, Mucorales, *Saksenaea vasiformis*, *Apophysomyces elegans*, *Trichophyton rubrum*, *Fusarium* spp., and *Coccidioides*, have been identified in marine hosts at least twice (Fig. 1d). Among these, *A. fumigatus* is the most frequently reported land-to-sea–transmitted fungal species. Its dispersal is facilitated by marine vegetation, coastal amphibians, and other shore-dwelling animals [93]. Despite its documented presence in marine environments, no genotyping studies have yet characterized *A. fumigatus* strains isolated from oceanic habitats [94].

6. Phylogenetic relatedness of terrestrial pathogens in marine hosts

Molecular studies have significantly enhanced our understanding of the terrestrial origins of certain pathogens, particularly *T. gondii*, by identifying key reservoirs and transmission routes into marine ecosystems. Numerous investigations have traced *T. gondii* from terrestrial sources, primarily felid hosts, to marine environments via freshwater runoff, often linking infection hotspots in marine wildlife to contaminated watersheds. Despite these advances, molecular evidence for many other terrestrial pathogens with potential marine impacts remains sparse. Expanding molecular surveillance and genomic analyses across a wider array of pathogens will be essential for elucidating transmission dynamics and evaluating their ecological risks in marine systems.

Phylogenetic analyses, which examine evolutionary relationships based on molecular data [95], offer powerful insights into the genetic relatedness of terrestrial pathogens identified in marine hosts. Analyses of conserved 16S rRNA gene sequences, for instance, suggest that many marine-associated bacteria, such as *Brucella* spp., are closely related to terrestrial strains (Fig. 2a). Most *Brucella* isolates from cetaceans cluster phylogenetically with those from terrestrial hosts including cattle, sheep, pigs, humans, and foxes. Interestingly, the dolphin-derived *Brucella* strain M292 shares 57 % genetic homology with terrestrial strains yet forms a distinct lineage, indicating evolutionary divergence.

Phylogenetic studies of viruses transmitted from land to sea reveal that marine morbilliviruses differ from their terrestrial counterparts, likely due to selective pressures encountered during cross-species transmission. Nevertheless, these viruses share a common ancestor, pointing to a clear evolutionary link between marine and terrestrial morbillivirus strains (Fig. 2b). Similarly, phylogenetic analyses of parasites indicate a high degree of genetic homology among *Sarcocystis* species found in seabirds, marine mammals, and terrestrial animals (Fig. 2c), further supporting the close evolutionary relationships between pathogens inhabiting terrestrial and marine environments.

7. Tracking the terrestrial origins of pathogens in marine animals

Phylogenetic analyses have provided valuable insights into the terrestrial origins of pathogens detected in marine animals. For *Brucella* species isolated from marine mammals, 16S rRNA sequence analysis reveals over 99 % genetic similarity with *Brucella* strains found in a wide range of terrestrial hosts, including dogs, cattle, buffalo, horses, sheep, goats, humans, vampire bats, yaks, freshwater fish, opossums, common voles, domestic pigs, and wild boars (Fig. 3a). This high degree of homology suggests a shared ancestry and implies that these terrestrial species may represent the original reservoirs for *Brucella* detected in marine environments.

In the case of marine-derived morbillivirus, the nucleocapsid protein gene exhibits the greatest sequence similarity, 97.87 %, to strains from Eurasian otters (*Lutra lutra*), followed by an 81 % similarity to human-derived strains (Fig. 3b). These results point to otters as the most likely primary terrestrial host, with humans potentially acting as a secondary source, though with marked genetic divergence.

Similarly, *Sarcocystis* species identified in marine animals share over 99 % sequence identity in their 18S rRNA genes with terrestrial strains from diverse hosts such as wild birds, dogs, chickens, raccoons, foxes, minks, badgers, otters, domestic pigs, wild fowl, wild boars, mice, goats, cattle, horses, freshwater fish, opossums, sheep, humans, and bears (Fig. 3c). This level of similarity supports the hypothesis of a shared evolutionary origin between marine and terrestrial *Sarcocystis* species, rather than recent zoonotic transmission events from land to sea.

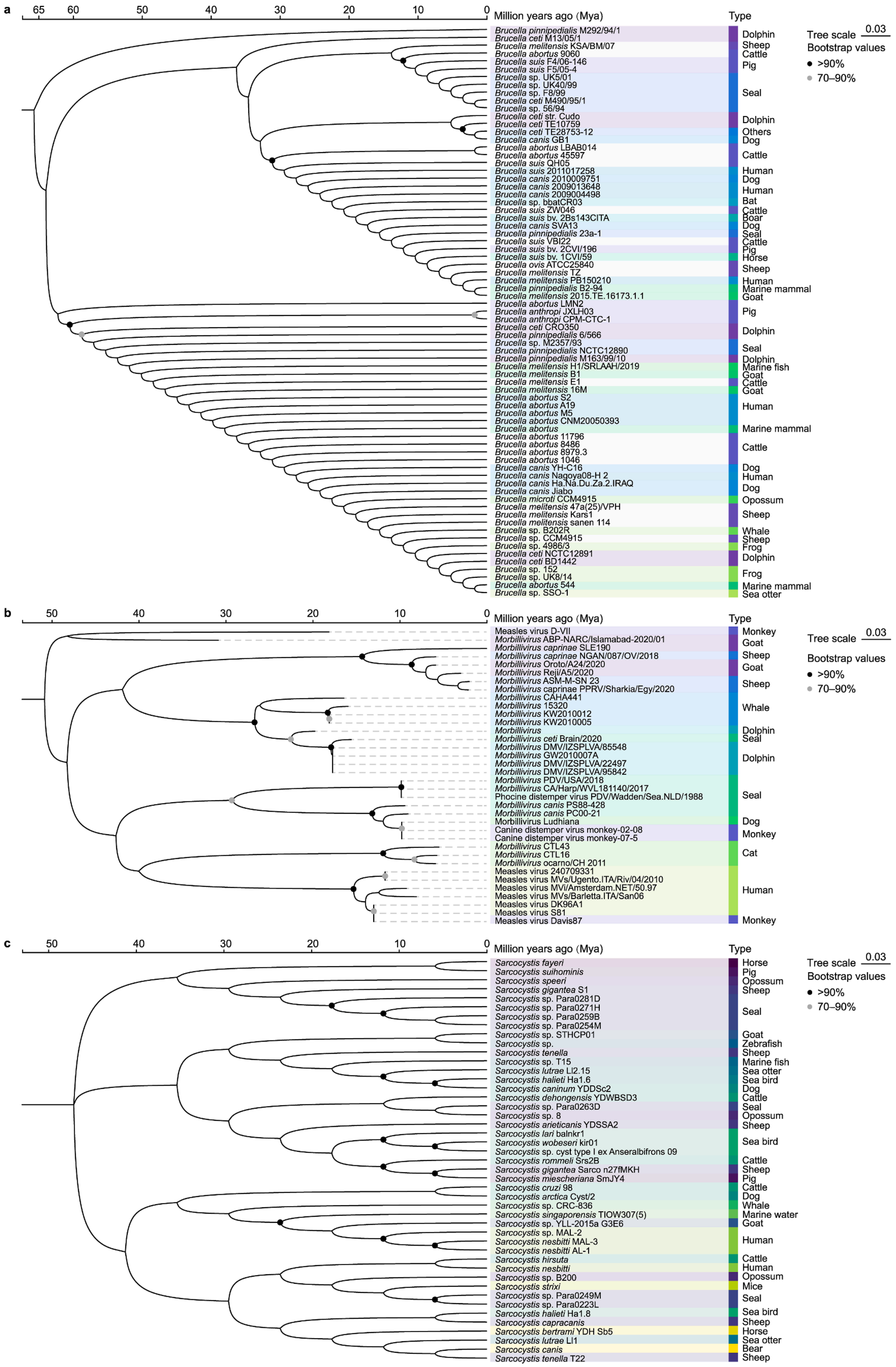
8. Transmission pathways

The ocean, a complex and biodiverse ecosystem, is continually influenced by terrestrial pathogens introduced through multiple transmission routes. These pathways are shaped by human activities, environmental change, food web dynamics, and vector-mediated transmission (Fig. 4). Below, we detail the primary routes through which terrestrial pathogens enter marine environments, highlighting their sources and supporting evidence.

Waste emission. Terrestrial pathogens are commonly introduced into marine systems through the discharge of sewage, industrial effluents, and agricultural runoff into rivers that ultimately flow into the ocean [96,97].

Weather and climatic events. Extreme weather events such as heavy rainfall, flooding, and mudslides facilitate the movement of pathogens from land to rivers and coastal waters [98]. Pathogens can adhere to sediments or particulate matter, which tides and floodwaters then transport into marine habitats [99–101].

Aerosol formation. Airborne transmission enables the dispersal of terrestrial pathogens—particularly fungi and spore-forming bacteria—into marine ecosystems [48]. These microorganisms may carry virulence factors and antibiotic resistance genes, impacting marine life similarly to their effects in terrestrial environments [102]. The deposition of terrestrial bioaerosols into the ocean involves several interconnected processes (Fig. 4). Bioaerosols, originating from soil, vegetation, microorganisms, and animal activity, are transported via atmospheric circulation.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Brucella pinnipedialis M292/94/1
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Brucella melitensis KSA/BM/07
Brucella abortus 9060
Brucella suis F4/06-146
Brucella suis F5/05-4
Brucella sp. UK5/01
Brucella sp. UK40/99
Brucella sp. F8/99
Brucella ceti M490/95/1
Brucella sp. 56/94
Brucella ceti str. Cudo
Brucella ceti TE10759
Brucella ceti TE28753-12
Brucella canis GB1
Brucella abortus LBAB014
Brucella abortus 45597
Brucella suis QH05
Brucella suis 2011017258
Brucella canis 2010009751
Brucella canis 2009013648
Brucella canis 2009004498
Brucella sp. bbatCR03
Brucella suis ZW046
Brucella suis bv. 2Bs143CITA
Brucella canis SVA13
Brucella pinnipedialis 23a-1
Brucella suis VBI22
Brucella suis bv. 2CVI/196
Brucella suis bv. 1CVI/59
Brucella ovis ATCC25840
Brucella melitensis TZ
Brucella melitensis PB150210
Brucella pinnipedialis B2-94
Brucella melitensis 2015.TE.16173.1.1
Brucella abortus LMN2
Brucella anthropi JXLH03
Brucella anthropi CPM-CTC-1
Brucella ceti CRO350
Brucella pinnipedialis 6/566
Brucella sp. M2357/93
Brucella pinnipedialis NCTC12890
Brucella pinnipedialis M163/99/10
Brucella melitensis H1/SRLAAH/2019
Brucella melitensis B1
Brucella melitensis E1
Brucella melitensis 16M
Brucella abortus S2
Brucella abortus A19
Brucella abortus M5
Brucella abortus CNM20050393
Brucella abortus
Brucella abortus 11796
Brucella abortus 8486
Brucella abortus 8979.3
Brucella abortus 1046
Brucella canis YH-C16
Brucella canis Nagoya08-H 2
Brucella canis Ha.Na.Du.Za.2.IRAQ
Brucella canis Jiabo
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Brucella ceti BD1442
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Brucella sp. UK8/14
Brucella abortus 544
Brucella sp. SSO-1
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Sheep
Cattle
Pig
Seal
Dolphin
Others
Dog
Cattle
Human
Dog
Human
Bat
Cattle
Boar
Dog
Seal
Cattle
Pig
Horse
Sheep
Human
Marine mammal
Goat
Pig
Dolphin
Seal
Dolphin
Marine fish
Goat
Cattle
Goat
Human
Marine mammal
Cattle
Dog
Human
Dog
Opossum
Sheep
Whale
Sheep
Frog
Dolphin
Frog
Marine mammal
Sea otter
b
50
40
30
20
10
0
Million years ago (Mya)
Type
Tree scale 0.03
Bootstrap values
● >90%
● 70–90%
Measles virus D-VII
Morbillivirus ABP-NARC/Islamabad-2020/01
Morbillivirus caprinae SLE190
Morbillivirus caprinae NGAN/087/OV/2018
Morbillivirus Oroto/A24/2020
Morbillivirus Reji/A5/2020
Morbillivirus ASM-M-SN 23
Morbillivirus caprinae PPRV/Sharkia/Egy/2020
Morbillivirus CAHA441
Morbillivirus 15320
Morbillivirus KW2010012
Morbillivirus KW2010005
Morbillivirus
Morbillivirus ceti Brain/2020
Morbillivirus DMV/IZSPLVA/85548
Morbillivirus GW2010007A
Morbillivirus DMV/IZSPLVA/22497
Morbillivirus DMV/IZSPLVA/95842
Morbillivirus PDV/USA/2018
Morbillivirus CA/Harp/WVL181140/2017
Phocine distemper virus PDV/Wadden/Sea.NLD/1988
Morbillivirus canis PS88-428
Morbillivirus canis PC00-21
Morbillivirus Ludhiana
Canine distemper virus monkey-02-08
Canine distemper virus monkey-07-5
Morbillivirus CTL43
Morbillivirus CTL16
Morbillivirus ocarno/CH 2011
Measles virus 240709331
Measles virus MVs/Ugento.ITA/Riv/04/2010
Measles virus MVi/Amsterdam.NET/50.97
Measles virus MVs/Barletta.ITA/San06
Measles virus DK96A1
Measles virus S81
Measles virus Davis87
Monkey
Goat
Sheep
Goat
Sheep
Whale
Dolphin
Seal
Dolphin
Seal
Dog
Monkey
Cat
Human
Monkey
c
50
40
30
20
10
0
Million years ago (Mya)
Type
Tree scale 0.03
Bootstrap values
● >90%
● 70–90%
Sarcocystis fayeri
Sarcocystis suihominis
Sarcocystis speeri
Sarcocystis gigantea S1
Sarcocystis sp. Para0281D
Sarcocystis sp. Para0271H
Sarcocystis sp. Para0259B
Sarcocystis sp. Para0254M
Sarcocystis sp. STHCP01
Sarcocystis sp.
Sarcocystis tenella
Sarcocystis sp. T15
Sarcocystis lutrae Ll2.15
Sarcocystis halieti Ha1.6
Sarcocystis caninum YDDSc2
Sarcocystis dehongensis YDWBSD3
Sarcocystis sp. Para0263D
Sarcocystis sp. 8
Sarcocystis arieticanis YDSSA2
Sarcocystis lari balnkr1
Sarcocystis wobeseri kir01
Sarcocystis sp. cyst type I ex Anseralbifrons 09
Sarcocystis rommeli Srs2B
Sarcocystis gigantea Sarco n27fMKH
Sarcocystis miescheriana SmJY4
Sarcocystis cruzi 98
Sarcocystis arctica Cyst/2
Sarcocystis sp. CRC-836
Sarcocystis singaporensis TIOW307(5)
Sarcocystis sp. YLL-2015a G3E6
Sarcocystis sp. MAL-2
Sarcocystis nesbitti MAL-3
Sarcocystis nesbitti AL-1
Sarcocystis hirsuta
Sarcocystis nesbitti
Sarcocystis sp. B200
Sarcocystis strixi
Sarcocystis sp. Para0249M
Sarcocystis sp. Para0223L
Sarcocystis halieti Ha1.8
Sarcocystis capracanis
Sarcocystis bertrami YDH Sb5
Sarcocystis lutrae Ll1
Sarcocystis canis
Sarcocystis tenella T22
Horse
Pig
Opossum
Sheep
Seal
Goat
Zebrafish
Sheep
Marine fish
Sea otter
Sea bird
Dog
Cattle
Seal
Opossum
Sheep
Sea bird
Cattle
Sheep
Pig
Cattle
Dog
Whale
Marine water
Goat
Human
Cattle
Human
Opossum
Mice
Seal
Sea bird
Sheep
Horse
Sea otter
Bear
Sheep

Extreme weather events such as storms and heavy precipitation can significantly increase aerosol deposition rates. This process is influenced by air quality and global climate change. However, considerable uncertainties remain regarding the transport, deposition, and reemission of bioaerosols in marine environments.

Future research should focus on identifying the sources of terrestrial bioaerosols, understanding their atmospheric transport and transformation in both coastal and open-ocean regions, investigating their diffusion patterns, retention times, and temporal (including seasonal and diurnal) variations, and exploring their interactions with marine aerosols during atmospheric transport and reentry. To accurately quantify these processes, long-term monitoring, remote sensing, and advanced tracking technologies will be essential. Additionally, further investigation should assess the broader ecological and health implications of bioaerosol emissions. Addressing these challenges will require an interdisciplinary approach that integrates field observations, numerical modeling, and emerging technologies to close existing knowledge gaps and enhance our ability to predict the impacts of bioaerosols on climate, marine ecosystems, and public health.

Maritime activities (human-mediated). Human activities at sea significantly contribute to the introduction of terrestrial pathogens. Large vessels and cruise ships discharge ballast water and human waste, which may carry diverse pathogens [103]. Tourism and recreational activities such as boating and diving also play a role. For example, *T. gondii* oocysts, shed in the feces of domestic and feral cats, can enter aquatic systems via sewage, stormwater runoff, or water currents in populated or tourist-heavy coastal regions. Once in the ocean, these oocysts can be dispersed by tides and currents, leading to exposure in susceptible marine species such as bivalves and sea otters. Furthermore, marine litter, particularly plastics, introduced through human activity can act as pathogen vectors. Contaminated debris transported by runoff or direct disposal may facilitate the spread of *T. gondii* and other pathogens such as *L. monocytogenes*, papillomaviruses, marine MVs, and *Schistosoma haematobium*.

Aquaculture (human-mediated). Marine and offshore aquaculture systems also serve as conduits for terrestrial pathogens such as *Salmonella* spp., *T. gondii*, *L. monocytogenes*, and influenza viruses. Contamination may arise from infected feed, untreated water, or runoff from land-based sources. Waste products from aquaculture, such as feces, uneaten feed, and carcasses, can harbor pathogens. Without proper waste management, these materials may facilitate transmission via water currents, aerosolization, or uptake by marine organisms [104,105].

Migratory birds. Seabirds and migratory species act as reservoirs for terrestrial pathogens, including influenza viruses. These viruses can reassort within avian populations [5,106,107], forming new variants that may spread into marine ecosystems, and potentially back into terrestrial populations [108,109].

Amphibians and coastal mammals. Species such as opossums and amphibians that dwell near coastlines can introduce pathogens such as *Mycobacterium* spp., *Sarcocystis* spp., *Leptospira*, and *Streptococcus* spp. into marine habitats [18,110–112].

Arthropods. Arthropods such as sea lice, mosquitoes, and crustaceans can act as vectors in pathogen transmission. For instance, mosquitoes may transmit viruses to marine mammals, while certain trematode parasites use crustaceans as intermediate hosts before infecting marine species [113,114].

Vertical transmission. Some terrestrial pathogens can be transmitted vertically, from parent to offspring, within marine animal populations. This enables their long-term persistence and dissemination in ocean environments [115].

Predatory activity. Pathogens may be transferred through marine food webs when infected animals are consumed or injured by predators. This mode of transmission has been observed in various marine species [116,117].

Runoff from snowmelt. Seasonal snowmelt can carry pathogens from terrestrial environments into rivers and, subsequently, into the ocean [118]. Conversely, marine-derived pathogens can also contaminate terrestrial freshwater sources when estuarine mixing, flooding, or tidal surges transport seawater inland [119]. Aquatic organisms and amphibians may further spread pathogens into freshwater habitats as they migrate or reproduce [120,121]. During heavy rainfall or flooding events, contaminated seawater may infiltrate terrestrial water storage systems, including groundwater aquifers, increasing the risk of pathogen transmission [122].

9. Impacts of terrestrially derived pathogens

9.1. Biodiversity of marine organisms

The introduction of terrestrial pathogens into marine ecosystems poses a significant threat to marine biodiversity. These disease-causing microorganisms, particularly those with zoonotic potential, can infiltrate aquatic environments, infect marine organisms, and compromise their immune responses. Marine animals often possess less robust immune defenses compared to their terrestrial counterparts, making them particularly susceptible to novel infections. Moreover, pathogen mutations that enhance survival and transmission in marine environments can exacerbate their impacts, leading to reduced reproductive success, increased disease susceptibility, and even large-scale mortality events [123–125]. In severe cases, such outbreaks may endanger entire populations, triggering cascading effects across marine ecosystems [126–128].

Marine ecosystems rely on intricate interspecies interactions that maintain ecological balance [129]. Apex predators such as marine mammals play a vital role in regulating food webs, but their health and population stability are increasingly jeopardized by terrestrial pathogen spillover [130]. Infections in these species can disrupt trophic dynamics and destabilize food chains, contributing to broader declines in biodiversity [131]. Additionally, terrestrial pathogens may outcompete native marine microbes for ecological niches and resources, thereby altering microbial community structures and further compromising ecosystem stability [132,133].

One of the most alarming consequences of terrestrial pathogen intrusion is the degradation of coral reef ecosystems. Land-derived pathogens have been linked to coral bleaching and mortality, posing a severe threat to reef biodiversity [134]. Certain RNA viruses originating from terrestrial sources have been shown to infect marine species, potentially altering host genetic diversity and facilitating genome reassortment [135]. These genetic changes may have unpredictable consequences for host resilience and disease susceptibility.

While stressors such as overfishing, habitat degradation, and climate change are well-established drivers of marine biodiversity loss, the contribution of terrestrial pathogens remains largely

Fig. 2. Phylogenetic relationships of terrestrially derived pathogens detected in marine organisms. Phylogenetic trees were constructed using the maximum likelihood method in RAxML (v.0.9.0), based on 16S rRNA gene sequences of *Brucella* spp. (**a**), nucleocapsid protein sequences of morbilliviruses (**b**), and 18S ribosomal gene sequences of *Sarcocystis* spp. (**c**). Node support was evaluated with 1000 bootstrap replicates. The resulting trees were visualized and annotated using iTOL.

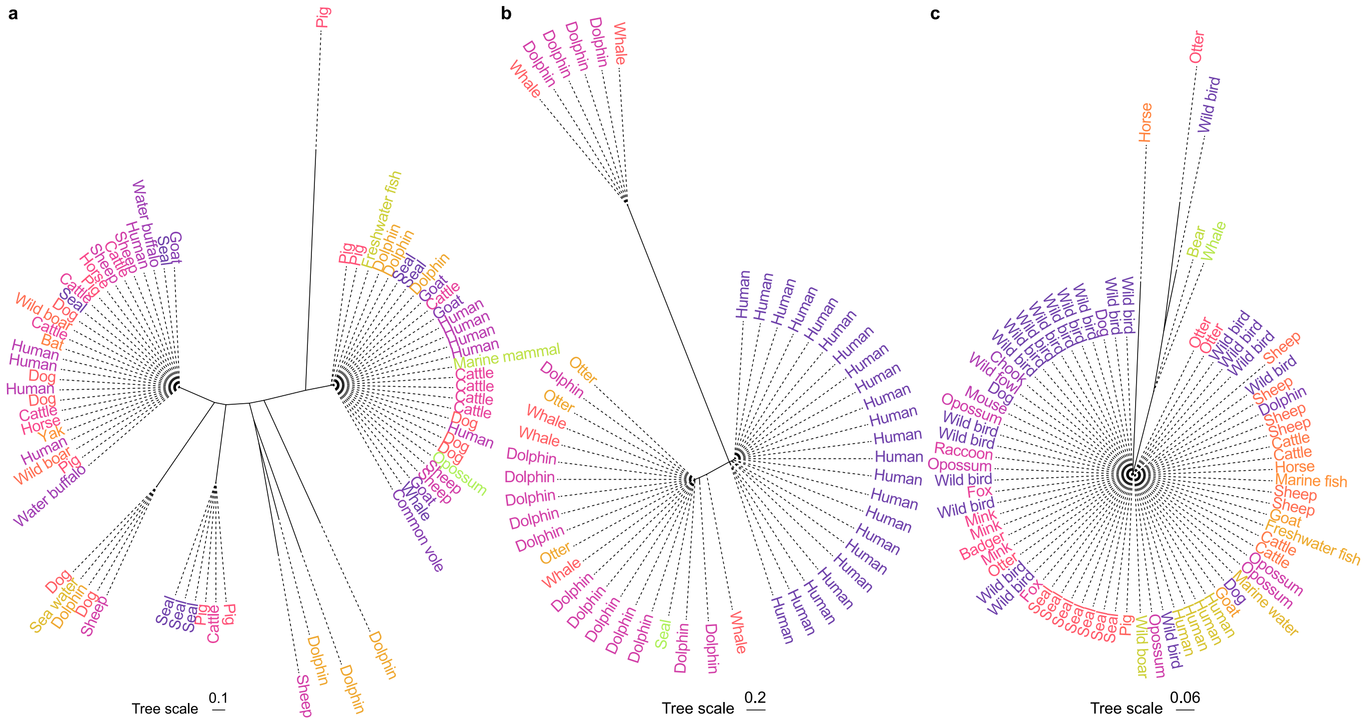

Fig. 3. Tracing terrestrial sources of marine animal pathogens. Phylogenetic analyses were conducted to investigate potential terrestrial origins of marine animal infections using sequences from three pathogen groups: 16S rRNA of *Brucella* spp. (**a**), nucleocapsid protein of *morbillivirus* (**b**), and 18S rRNA of *Sarcocystis* spp. (**c**). Sequences were aligned using MEGA7 (v7.0.26), and maximum likelihood phylogenetic trees were generated with RAxML (v0.9.0) using 1000 bootstrap replicates to assess node support. Scale bars indicate evolutionary distance. Sequence data used for tree construction are listed in Supplementary Table S2–4.

underexplored. For example, sea cucumber populations have experienced sharp declines due to overexploitation and coastal development. Although evidence directly linking terrestrial pathogens to genetic erosion in sea cucumbers is limited, González-Wangüemert et al. [136] demonstrated that overharvesting significantly reduces their genetic diversity, increasing their vulnerability to external pressures. Similarly, research by Soliman et al. [137,138] and Hamamoto et al. [139] highlights the impacts of coastal development and environmental change on sea cucumber populations. While studies such as Wingfield et al. [140] have reported fungal infections in sea cucumbers, a definitive link between terrestrial pathogen spillover and population decline has yet to be established. The possibility that such pathogens contribute to genetic erosion in marine invertebrates remains an open and important area for future research.

Beyond direct infections, terrestrial pathogen introduction can trigger broader ecosystem-level disruptions. Pathogen transmission through marine food webs can alter trophic structures, disrupt energy flow, and impair ecosystem functioning [141]. In California, for instance, the decline of conch populations was attributed to seaweed contaminated by terrestrial pathogens. This led to reduced numbers of conch predators and a weakened algal community, ultimately destabilizing the local ecosystem. Similarly, in Australia, terrestrial pathogens have been implicated in coral reef degradation, resulting in habitat loss and widespread disruption of marine food chains [142,143]. These findings collectively highlight the urgent need to assess and mitigate the impacts of terrestrial pathogens on marine biodiversity. While environmental and anthropogenic stressors are widely acknowledged, the overlooked role of pathogen spillover from land to sea warrants more scientific and policy attention to ensure the health and resilience of marine ecosystems.

9.2. Public and environmental health

Terrestrially derived pathogens introduced into marine environments can pose serious risks to both public and environmental health. These pathogens may be transmitted back to humans through recreational and occupational activities such as swimming, diving, and fishing. Examples include *Brucella* spp., *Vibrio maritimus*, *T. gondii*, influenza viruses, and hepatitis viruses, which can spread through direct contact with contaminated seawater [144–146]. Coastal populations and offshore workers are particularly vulnerable, as these pathogens can infiltrate marine systems and re-enter human communities through routes such as contaminated drinking water or seafood consumption [147–150]. A significant consequence of this reverse transmission is the contamination of water and soil. [151]. For example, the use of pathogen-contaminated water for irrigation can lead to the contamination of crops and potable water supplies, creating an indirect route for human infection. Livestock and poultry exposed to such contaminated resources may also become reservoirs, further facilitating the transmission of disease to humans. A key example is *L. monocytogenes*, a foodborne pathogen capable of spreading through irrigation water, contaminating produce, and entering the food chain—ultimately posing a risk to human health [152]. Moreover, contaminated water can seep into surrounding soils and freshwater systems, affecting rivers, lakes, groundwater, and terrestrial wildlife. This broad environmental contamination can have long-term ecological impacts. In rural areas of China, for example, prolonged consumption of groundwater polluted by environmental pathogens has been linked to serious health issues, including cancer and liver disease [153].

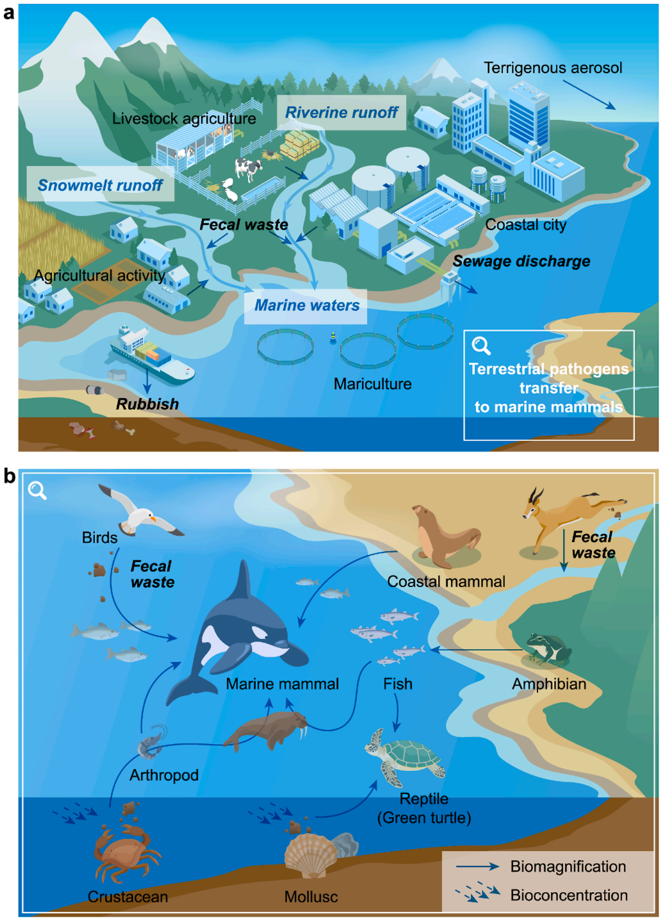

Fig. 4. Conceptual overview of terrestrial pathogens transmission pathways to the marine environment. **a**, Pathways by which terrestrial pathogens are transferred to marine mammals via human activities. Arrows illustrate pathogen movement through multiple routes, including atmospheric transport (terrigenous aerosols), riverine runoff (from snowmelt and surface water), and direct coastal inputs (e.g., sewage discharge, agriculture, and mariculture). Weather events such as storms and precipitation can intensify pathogen transport through air and water pathways. **b**, Pathways of terrestrial pathogens within marine environment. Pathogens interact with coastal and marine organisms, such as mollusks, crustaceans, fish, amphibians, sea turtles, seabirds, and marine mammals, potentially facilitating further spread within oceanic ecosystems. Oceanic processes such as currents and mixing influence pathogen distribution and persistence, while factors such as climate change and air quality variations further affect transmission dynamics.

10. Future research directions

Despite considerable advances in understanding the mechanisms by which terrestrial pathogens are transmitted to marine environments, numerous critical questions remain unanswered. These knowledge gaps underscore the need for continued research into the complex dynamics of pathogen spillover and persistence in marine ecosystems. One key priority is sustained surveillance to uncover the evolutionary drivers behind transmission events and pathogen adaptation in marine hosts. Equally important is the development of more sensitive and reliable detection methods, as existing techniques often lack the precision needed to accurately quantify pathogen abundance and distribution in marine settings. Raising public and scientific awareness about the health and ecological consequences of terrestrial pathogens in marine environments is essential—particularly in low- and middle-income countries, where environmental contamination is frequently underreported and under-monitored. In these regions, limited resources can hinder both data collection and public health response. Moreover, research into the transmission dynamics of terrestrial pathogens within marine ecosystems remains in its infancy. There are significant gaps in our understanding of how these pathogens interact with marine species, influence host susceptibility, and evolve within aquatic environments. Investigating their ecological and evolutionary impacts, such as shifts in microbial communities, disease emergence, and biodiversity loss, is essential for informing mitigation strategies. Ultimately, future research must prioritize the development of targeted control measures to prevent and reduce land-to-sea pathogen transmission. This includes interdisciplinary efforts that integrate environmental monitoring, molecular biology, oceanography, and public health to safeguard marine biodiversity and human well-being.

11. Conclusion

Terrestrially derived pathogens are increasingly recognized as pervasive contaminants in marine environments. However, significant uncertainties remain regarding their sources, transmission pathways, and ecological consequences. This review has examined the transmission dynamics, ecological impacts, and distribution of key terrestrial pathogen groups, including bacteria, viruses, parasites, and fungi, that infiltrate marine ecosystems. These pathogens can move in both directions: from land to sea and, in some cases, from sea back to land. This bi-directional transmission increases the risk of cross-species infection and zoonotic spillover. Many of these pathogens possess zoonotic potential, and some may undergo adaptive mutations that enable them to infect marine organisms, posing a serious threat to marine biodiversity. However, not all pathogens exhibit the same capacity for mutation and adaptation in aquatic environments. Their potential for evolutionary change is influenced by both pathogen-specific biological traits and the surrounding environmental conditions. Infections caused by terrestrial pathogens can be particularly severe in marine mammals, leading to population declines and disrupting ecological balance. A deeper understanding of the biodiversity, taxonomy, and host range of these pathogens in marine organisms is essential for tracing their evolutionary trajectories and identifying the routes of land-to-sea transmission. Mitigating the spread of land-based pathogens into marine environments demands a multidisciplinary and collaborative approach. Key strategies include enhancing environmental surveillance, improving wastewater treatment and coastal infrastructure, and integrating public health and ecological monitoring systems. Cross-sectoral and international cooperation, along with ecosystem restoration efforts, are vital to reducing pathogen transmission risks. Furthermore, raising public awareness, developing predictive disease models and early warning systems, and establishing a robust, integrated prevention and response framework are critical steps toward safeguarding both public health and marine ecosystems from the growing threat of terrestrial pathogens.

CRediT authorship contribution statement

Hai-Chao Song: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Software, Visualization. **Hany Elsheikha:** Writing – review & editing, Validation, Conceptualization, Investigation, Methodology. **Tao Yang:** Software, Writing – review & editing. **Wei Cong:** Writing – review & editing, Validation, Project administration, Funding acquisition, Conceptualization, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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