Integrating climate change, biological invasions, and infectious wildlife diseases

David W Thieltges[1,2*], David Bruce Conn[3,4], Ross N Cuthbert[5], Alison M Dunn[6], E Rosa Jolma[1,7], M Camille Hopkins[8], Volodimir Sarabeev[9,10], Sander Smolders[11], Carol A Stepien[12], K Mathias Wegner[13], and Patrick M Kočovský[8]

Climate change is likely to affect infectious diseases that are facilitated by biological invasions, with repercussions for wildlife conservation and zoonotic risks. Current invasion management and policy are underprepared for the future risks associated with such invasion-related wildlife diseases. By considering evidence from bioclimatology, invasion biology, and disease research, we illustrate how climate change is anticipated to affect disease agents (parasites and pathogens), hosts, and vectors across the different stages of invasions. We highlight the opportunity to integrate these disciplines to identify the effects of climate change on invasion-related wildlife diseases. In addition, shifting to a proactive stance in implementing management and policy, such as by incorporating climate-change effects either into preventative and mitigation measures for biosecurity or with rapid response protocols to limit disease spread and impacts, could help to combat future ecological, economic, and human health risks stemming from invasion-related wildlife diseases.

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Invasive species and climate change are two major threats to global biodiversity and ecosystem services, with resultant economic losses and control efforts costing billions annually (Diagne *et al*. 2021; IPBES 2023). Among the impacts of invasive species is their potential to affect infectious diseases through a variety of mechanisms (*invasion-related wildlife diseases*; for details, see Appendix S1: Panel S1). Invasive parasites (here broadly defined as all parasitic and pathogenic organisms, including eukaryotes, prokaryotes, and viruses) can either be co-introduced with their hosts/vectors or be introduced while in free-living infective stages. Furthermore, invasive species can be novel hosts or vectors for native parasites, facilitating their spread in recipient ecosystems. Introductions of parasites can lead to emerging diseases in wildlife, livestock, and aquaculture and may pose zoonotic risks for humans (Hatcher *et al*. 2012; Conn 2014; Roy *et al*. 2023).

In a nutshell:

- Climate change can affect biological invasions and invasion-related infectious diseases, creating ecological, economic, and health risks for wildlife, domesticated species, and humans
- Understanding how climate change can alter invasion-related wildlife diseases requires the integration of climate change-, biological invasion-, and disease-focused disciplines in ecological, veterinary, and medical sciences
- Management and policy actions can help to anticipate climate-change effects on invasion-related wildlife diseases, with the aim to improve existing prevention, detection, eradication, containment, and mitigation measures at all stages of the invasion process and with a particular focus on preventative measures

Invasion processes and parasite–host interactions are both affected by several aspects of climate change, including extreme weather events such as heat waves, droughts, storms, or floods (Harvell *et al*. 2002; Walther *et al*. 2009; Diez *et al*. 2012; Altizer *et al*. 2013; Marcogliese 2016; Claar and Wood 2020). Understanding how climate change will affect invasion-related wildlife diseases will require integration of research on climate change, biological invasions, and diseases (Figure 1). Appropriate management and policy actions can help to mitigate the impact of climate change on invasion-related wildlife diseases. To that end, the current governance structure, in which different aspects are covered by separate policymaking organizations, could be adapted to incorporate integrated research into management and policy (Figure 1; Roy *et al*. 2017).

Here we consider evidence from bioclimatology, invasion biology, and disease research to illustrate how climate change can affect not only the different stages in the invasion process of parasites, hosts, and vectors but also disease emergence and impacts. We highlight research gaps and their potential management and policy implications, which could be addressed

[1]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, the Netherlands [*](david.thieltges@nioz.nl); [2]Groningen Institute for Evolutionary Life-Sciences, University of Groningen, Groningen, the Netherlands; [3]One Health Center, Berry College, Mount Berry, GA; [4]Department of Invertebrate Zoology, Museum of Comparative Zoology, Harvard University, Cambridge, MA; [5]Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, Belfast, UK; [6]Faculty of Biological Sciences, University of Leeds, Leeds, UK; [7]Department of Population Health Sciences, Veterinary Medicine, Utrecht University, Utrecht, the Netherlands;

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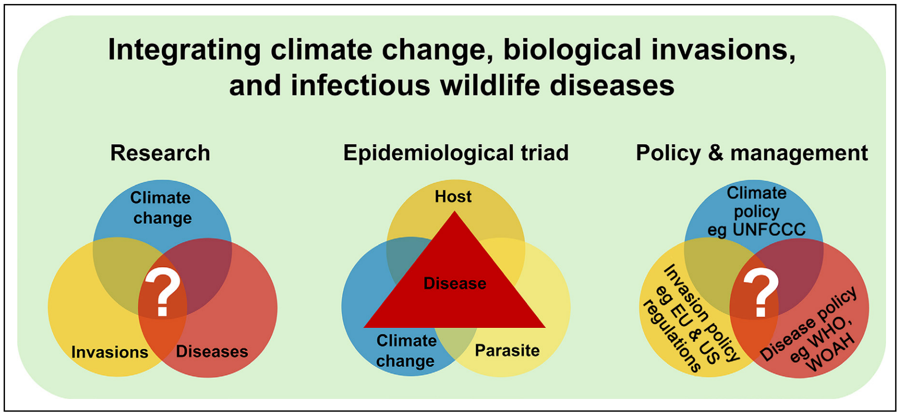

Figure 1. Integration of research on climate change, biological invasions, and diseases (left) can help not only to identify the likely effects of climate change on invasion-related wildlife diseases, as captured in the classic epidemiological triad (middle), but also to develop appropriate policy and management actions (right), which currently are siloed and focus only on single aspects: for instance, climate-specific policies by the UN Framework Convention on Climate Change (UNFCCC), invasion-specific regulations by the European Union (EU) and the US, and disease-specific policies by the World Health Organization (WHO) and the World Organisation for Animal Health (WOAH).

through integrated research on and management of the effects of climate change on invasion-related wildlife diseases.

Climate effects on parasite–host interactions and diseases

Climate change has been linked to increased risk for many wildlife and human infectious diseases (Harvell *et al.* 2002; Mora *et al.* 2022), but the relationship between climate and infectious disease is often complex (Lafferty 2009; Rohr *et al.* 2011; Altizer *et al.* 2013; Cohen *et al.* 2020). In general, climate effects on disease risks result from shifts within the epidemiological triad through changes in environmental conditions or in the traits and abundances of hosts and parasites, which can have direct and indirect effects on infectious diseases (Figure 1). On the host side, changes in temperature, precipitation, and other climate-related factors can affect host survival and reproduction, and ultimately host population size, along with host immune system function relevant for parasite–host interactions (Figure 2; Hing *et al.* 2016). In ectothermic hosts, temperature affects immune responses directly, with some species using behavioral fever or the deliberate movement to warmer environments to combat infections by increasing body temperature (Rakus *et al.* 2017; Turner *et al.* 2021). Climate change may alter this capacity for behavioral temperature regulation.

For parasites with complex life cycles or those that are vector-borne, disease dynamics can be directly and indirectly altered through climate-change effects on intermediate hosts or vectors, as well as on parasitic stages within and free-living transmission stages originating from hosts (Figure 2; Barber *et al.* 2016). For example, higher temperatures can promote elevated production and release of infective free-living parasite stages, such as in trematodes (Poulin 2006), which in turn frequently exhibit reduced survival at elevated temperatures along with higher infectivity in subsequent hosts (Barber *et al.* 2016). However, the temperature effects on metabolic processes of ectothermic species follow a thermal performance curve with a limited operational temperature range for each species (Phillips *et al.* 2022). Free-living infective stages can also be affected by other climate-change–related factors such as desiccation and salinity shifts due to altered precipitation patterns (Pietrock and Marcogliese 2003). Likewise, vectors can be affected by climate change and may exhibit extended seasonal occurrence and produce more generations at higher temperatures (Ogden and Lindsay 2016; Cuthbert *et al.* 2023). Finally, climate change can affect species that do not serve as competent hosts or vectors but instead act as facilitators or inhibitors of parasite–host interactions (Figure 2). For example, in cases where climate influences the abundance of plants that provide substrate for infective stages (or hosts and vectors), this may affect parasite transmission and alter disease dynamics. Alternatively, non-host species can act as inhibitors by removing parasites from the pool of infective stages via predation, with increased temperatures potentially affecting the consumption rate, particularly for ectothermic consumers (Johnson *et al.* 2010). Therefore, all stages in the transmission cycle of parasites can potentially be impacted by climate change, although knowledge about which stages are critical is sparse.

In addition to affecting parasite–host interactions, climate change can also facilitate the spread of parasites, hosts, and vectors. Climate-change–induced range shifts by hosts and vectors, as well as altered migratory behavior (Shaw 2016), can redistribute parasites and create new niches for those parasites that are already present. Increasing frequency and magnitude of extreme weather events and subsequent increased dispersal of artificial materials, such as plastics, could promote long-distance transport of taxa that include parasites, hosts, and vectors (eg blown by storms, transported long distances by flood currents or on debris; Diez *et al.* 2012). One example is the long-distance transport of terrestrial fungal spores across the Atlantic Ocean by African dust storms, through which potential coral pathogens can be introduced into the Caribbean Sea (Weir-Brush *et al.* 2004). Likewise, infective stages causing waterborne diseases may show increased dispersal and transmission during extreme weather events, such as storms or floods (Cann *et al.* 2013).

Climate-change effects on different stages in the invasion process

Biological invasions fundamentally occur in stages, from transport to introduction into a recipient ecosystem, followed by establishment and spread with potential impacts (Figure 3; Blackburn *et al.* 2011). Parasite invasions typically also move through these stages and intervention measures can be applied at each stage (Dunn and Hatcher 2015). Climate change can affect parasites, hosts, and vectors during these different stages, leading to changes in the dynamics of invasion-related diseases (Figure 3).

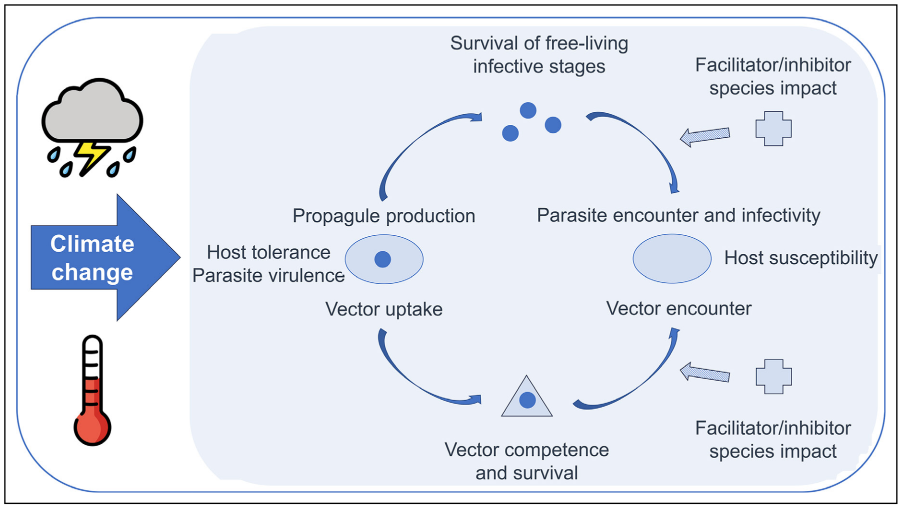

Figure 2. Climate-change phenomena, such as rising temperatures and extreme weather events, can affect wildlife diseases by altering various infection-related traits of parasites (solid circles) and hosts/vectors (ovals and triangle), as well as mediating the impact of facilitator and inhibitor species (crosses) on parasite transmission. Thermometer and cloud icons designed by OpenMoji.org (CC BY-SA 4.0).

Transport

Transport of species to recipient ecosystems is the starting point of all biological invasions (Figure 3). In general, species can be transported intentionally (eg as pets or for farming, gardening, or aquaculture) but, in the absence of biosecurity, they can also be transported unintentionally as stowaways (eg in wood or soil, on/in organisms, on plastics and vessel hulls, or in ballast water) (Canning-Clode 2015). Some parasites are unintentionally transported with their hosts or vectors, whereas others are intentionally introduced to control pests (Roy *et al.* 2011). However, hosts often arrive without their parasites (parasite release; Torchin *et al.* 2003). This stems from stochastic effects (the source individuals may not be infected) or from selective pressures during transport (lower survival rates among infected individuals). Transport of parasites, hosts, or vectors can also occur after a successful initial introduction, due to human-mediated transport in the recipient region, leading to secondary introductions, or by range expansion through natural dispersal.

Climate change has strong potential to affect the transport stage in the invasion process. At the source, elevated infection levels of parasites or larger population sizes of hosts or vectors due to climate change may increase the chances of infected individuals being transported. Climate change can also affect the transport pathways themselves. For example, new polar shipping routes (Ware *et al.* 2016) and the construction of new waterways, such as canals for irrigation and to offset drought-related shortages of potable water (Galil *et al.* 2008), can create new transport pathways.

Environmental conditions impacted by climate change may affect the survival of parasites, hosts, and vectors undergoing transport (eg via ballast water and shipping containers, at ports of entry, and so on). Depending on the species, these conditions can either reduce or increase survival, which will ultimately affect propagule pressure (frequency, quantity, and quality of introduced immature or adult stages) in recipient ecosystems, which is known to be a pivotal driver of introduction success (Simberloff 2009). Altered environmental conditions during transport could also lead to selection of individuals with particular traits that improve the likelihood of invasion success (eg generally wider tolerance to stressors associated with transport; Briski *et al.* 2018). In addition, for particular invasion pathways such as new polar shipping routes, duration of travel to recipient ecosystems may be shortened, which may increase parasite, host, and vector survival.

Introduction and establishment

After surviving transport to recipient ecosystems, newly arrived parasites, hosts, or vectors might become introduced and eventually establish self-sustaining populations (Figure 3). In general, the major obstacles for introduction and establishment are environmental constraints in the form of abiotic conditions (environmental requirements of the species) and biotic interactions with native communities (the native community may show biotic resistance against non-native organisms through competition, predation, or parasitism; Zenni and Nuñez 2013). Given that abiotic factors such as temperature have strong effects on parasite–host interactions, climate change is likely to affect invasion-related diseases at the introduction and establishment stages (Figure 3).

The likelihood of introduction is increased if the abiotic conditions of the recipient ecosystem are similar to the requirements of the invading parasites, hosts, and vectors—introduction can be further influenced by the capacity of non-native species within their native (source) regions to become pre-adapted to conditions within the recipient ecosystem prior to the invasion thereof (Briski *et al.* 2025). More

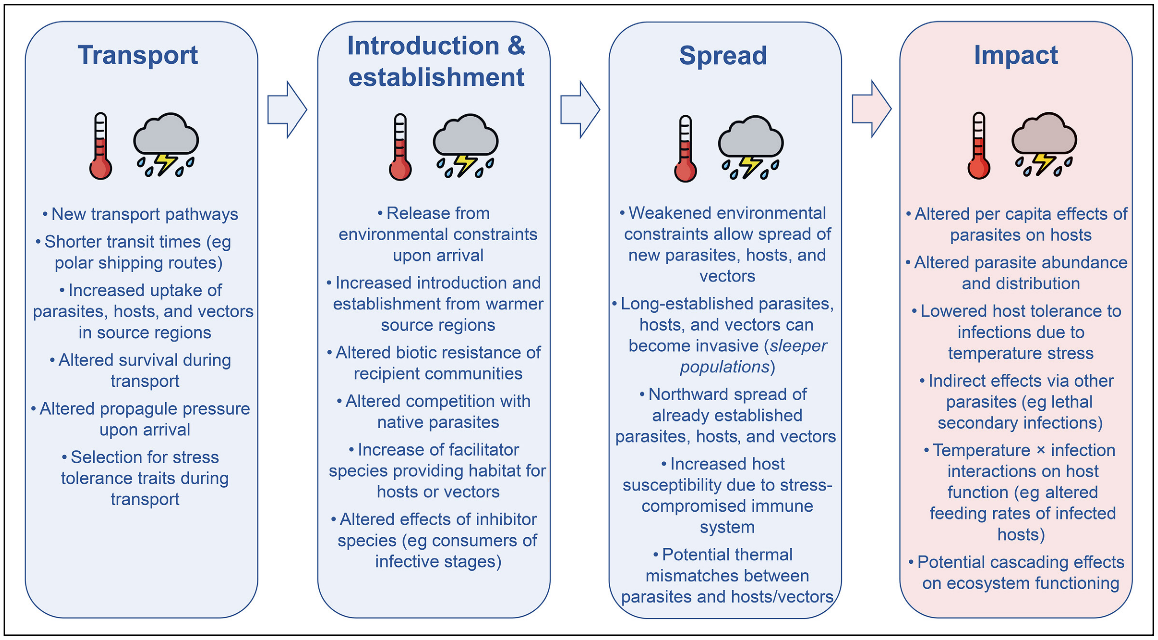

Figure 3. The four stages of the invasion process—transport, introduction & establishment, spread, and impact—for parasites, hosts, and vectors, with examples of the mechanisms through which climate change can affect invasion-related wildlife diseases at each stage. See main text for details. Thermometer and cloud icons designed by OpenMoji.org (CC BY-SA 4.0).

importantly, to ensure subsequent establishment, the abiotic conditions of recipient ecosystems must be suitable for reproduction and maintaining self-sustaining populations. For example, many parasites, hosts, and vectors transported from tropical/subtropical to temperate ecosystems are likely constrained by mismatched climatic niches and the abiotic conditions in recipient ecosystems. Climate change coupled with urbanization may release newcomers from such constraints and thus lead to increased introductions and establishment of species from warmer source regions. For example, recent warming has led to secondary introductions of the Asian tiger mosquito (*Aedes albopictus*), originally from tropical and subtropical habitats, to northern regions in Europe, possibly resulting from increasingly favorable climatic conditions therein (Oliveira *et al.* 2021). This species is an important vector of domestic animal and zoonotic diseases, and its establishment in northern Europe may increasingly allow for the introduction and establishment of accompanying parasites, including heartworm and those causing other zoonotic diseases (eg West Nile virus, Zika, yellow fever, dengue fever, Chikungunya fever; Benedict *et al.* 2007).

In addition to affecting the distribution and abundance of hosts and vectors, climate change might alter parasite–host interactions. For instance, higher temperatures may release infection barriers in hosts and vectors in concert with faster parasite replication, which can enable parasite introduction and establishment. An example of this is the common house mosquito *Culex pipiens*, a competent vector of the zoonotic West Nile and Usutu viruses introduced to Europe, with northward secondary introductions by or natural range expansions of those viruses currently limited by their temperature tolerances (Vogels *et al.* 2017). Climate change may also affect competition between invasive and native parasites, as parasite–parasite interactions are potential drivers of infection dynamics (Telfer *et al.* 2010). For example, a climate-associated decline in native parasite abundance may open niche space for newly arrived non-native parasites. In contrast, a climate-associated increase in native parasite abundance may alter interspecific interactions and thereby affect the introduction and establishment of newly arrived non-native parasites.

Finally, native and invasive species that do not serve as competent hosts themselves could also alter the introduction and establishment of parasites, hosts, and vectors. For instance, the predicted introductions of the invasive water hyacinth *Pontederia crassipes*, which provides breeding habitat for mosquitoes that serve as a vector for a range of human diseases, could expand the ranges of those diseases (Bojko *et al.* 2023). In contrast, species that interfere with parasite transmission (eg by consuming infective parasite stages) may impede parasite introduction and establishment, since consumption rates often increase with temperature up to a given thermal optimum (Goedknegt *et al.* 2015).

Spread of new and long-established parasites, hosts, and vectors

Environmental constraints also play a crucial role in the further spread of both newly established and long-established non-native parasites, hosts, and vectors (Figure 3). When such constraints are weakened under climate change, these species may thrive (*sleeper populations/species*; Spear *et al*. 2021), so much so that they eventually become invasive (sensu Blackburn *et al*. 2011). However, when environmental constraints are strengthened under climate change, these species may decline.

Climate-change impacts will affect not only the population dynamics of—and interactions between—parasites, hosts, and vectors, but also their ability to spread within recipient ecosystems. For parasites, propagule production can increase under warmer conditions, which could facilitate population growth and spread (Poulin 2006). For hosts, temperature stress may weaken immune responses and enhance susceptibility to parasites, facilitating their spread (Hing *et al*. 2016). However, these effects are not universal and vary by parasite and habitat, making it difficult to generate broad predictions (Cohen *et al*. 2020). Furthermore, climate-change–associated thermal mismatches may affect parasite–host interactions, resulting in increases or decreases in disease risk under climate change (Rohr and Cohen 2020). For example, infection by the invasive marine parasitic rhizocephalan barnacle *Loxothylacus panopaei* reduces the survival of its native crab host under elevated temperatures, and the ensuing decline in hosts is predicted to lead to local parasite extinctions with 2°C warming (Gehman *et al*. 2018). Another complex example is the impact of temperature on the invasive fungus *Batrachochytrium dendrobatidis* (Bd), which causes chytridiomycosis in amphibians and is partly responsible for global amphibian declines (Turner *et al*. 2021). Temperatures between 17°C and 25°C are optimal for Bd growth, but temperatures above 28°C are lethal to the fungus; furthermore, host mortality is often lower at higher temperatures because of improved immune responses (Turner *et al*. 2021). Temperature increase can also negatively affect the host's microbiome and its effect in modulating infection intensity and disease severity (Bernardo-Cravo *et al*. 2020). The parasite *Perkinsus marinus* has a narrower temperature range than its host, the economically important eastern oyster *Crassostrea virginica*; hence, infection is limited to oyster populations in warmer water temperatures. However, disease outbreaks coinciding with warming ocean temperatures have been found to cause high mortality in previously uninfected oyster populations (Cohen *et al*. 2018). These examples reinforce the view that the direction and magnitude of climate-change effects on invasion-related wildlife diseases will vary across parasite–host systems and recipient ecosystems.

Altered impacts under climate change

The impact of an invader is defined by the combination of its per capita effect, its range size, and its abundance (Parker *et al*. 1999). When climate change affects the range or abundance of parasites, hosts, or vectors (see "Introduction and establishment" and "Spread of new and long-established parasites, hosts, and vectors" sections above), or their per capita effects, this can have consequences for invasion-related diseases (Figure 3). Similarly, parasitism can interact with climate change to worsen the impacts of invasive species in ways that cannot be predicted by stressor considerations in isolation, for both per capita and population-level effects (Laverty *et al*. 2017; Faria *et al*. 2023).

With respect to influencing the per capita effect of a parasite on its host, climate change can alter not only the parasite's infectivity, pathogenicity, and virulence but also the host's susceptibility and tolerance. For example, rising temperatures can increase the energetic demands of the parasite, which may lead to increased feeding on—and negative fitness consequences for—the host (and in some cases also lead to parasite replication) (Kirk *et al*. 2018). For the host, rising temperatures can constitute environmental stress that can lower its immune response, which increases its susceptibility and reduces its tolerance to infection (Claar and Wood 2020). However, the degree of impact will depend on whether the host is an ectotherm or an endotherm, as well as the season (if the increase in temperature occurs within the species' operational temperature range or at its upper limit; Phillips *et al*. 2022); for instance, for hosts in temperate habitats, higher temperatures in summer might be stressful, whereas higher temperatures in winter could be beneficial. Combined effects of infection and temperature on host immunity might also lead to indirect effects on other parasites. For example, under elevated temperature conditions, an invasive marine intestinal copepod (*Mytilicola intestinalis*) increases the susceptibility of native mussel hosts to lethal secondary bacterial infections (*Vibrio* spp) (Demann and Wegner 2019).

Interactions between parasites and climate change can also alter the impacts of invasive hosts on native biota. For instance, invasive freshwater amphipods (*Gammarus pulex*) infected with an acanthocephalan parasite (*Echinorhynchus truttae*) exhibit elevated feeding rates on their prey at high temperatures, similar to predicted future temperatures, as compared to uninfected conspecifics (Laverty *et al*. 2017); however, these effects might be counteracted at the population level by reductions in amphipod abundance. Biotic contexts, such as evolutionary experience and trophic naïveté, can further influence feeding rates on intermediate hosts (Sheath *et al*. 2018), warranting further examination in a climate change and invasion context. For native biota, the combined impact of climate change and invasion-related wildlife diseases can also extend beyond the respective parasite–host interaction, leading to cascading effects in invaded ecosystems. For example, seagrass wasting disease, caused by invasive protists (*Labyrinthula* spp), is associated with marine heatwaves (Aoki *et al*. 2022) and the resulting seagrass die-off can have cascading effects on invertebrate populations, waterbirds, and carbon sequestration (Muehlstein 1989).

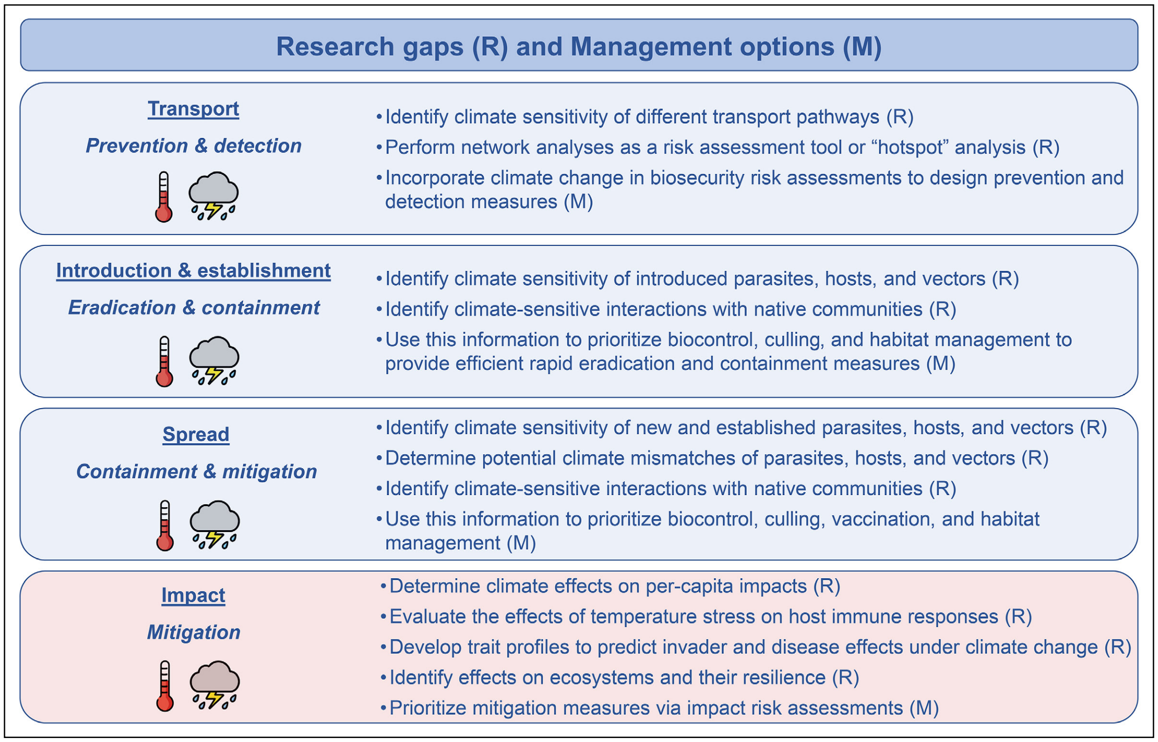

Figure 4. Potential implications of climate-change effects on invasion-related diseases for research gaps and management options, sorted by the different stages of the invasion process for parasites, hosts, and vectors. Thermometer and cloud icons designed by OpenMoji.org (CC BY-SA 4.0).

Conclusions

Climate change is likely to affect biological invasions and invasion-related diseases in many ways, with important repercussions for wildlife conservation and zoonotic risks. However, climate-change impacts will not be universal but will instead differ among parasite–host systems and recipient ecosystems. To better understand the underlying mechanisms, we highlight the opportunity to integrate the disciplines of climate change, biological invasions, and disease research (Figures 1 and 4). Integrated and transdisciplinary research can help to identify the climate sensitivity of parasites, hosts, and vectors at different stages of the invasion process (Figure 4). In addition, determining the climate sensitivity of interactions with native communities can provide information on their resilience to invasions by parasites, hosts, and vectors, as well as the impacts incurred (Figure 4). This knowledge can then be used to anticipate climate-change effects on invasion-related diseases to inform actionable management and policy (Figure 4). Identifying high-risk situations as precisely and early as possible can support successful disease risk management. One approach is to shift from reactive to proactive stances (Cuthbert *et al.* 2022), such as incorporating climate-change effects in preventative biosecurity and risk assessment measures or in rapid response protocols aimed at limiting disease spread and impact (Figure 4). Although their implementation may be challenging, given the complexity of climate change, such recommendations can help to combat future ecological, economic, and health risks stemming from invasion-related wildlife diseases.

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Data Availability Statement

No data were collected for this study.

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[8]*US Geological Survey, Office of the Associate Director for Ecosystems, Reston, VA;* [9]*Department of Biology, Zaporizhzhia National University, Zaporizhzhia, Ukraine;* [10]*Institute of Parasitology, Slovak Academy of Sciences, Košice, Slovak Republic;* [11]*Ministry of Infrastructure and Water Management, The Hague, the Netherlands;* [12]*National Museum of Natural History Research Associate, Smithsonian Institution, Washington, DC;* [13]*Alfred Wegener Institute–Helmholtz Centre for Polar and Marine Research, Coastal Ecology, Wadden Sea Station Sylt, List, Germany*

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