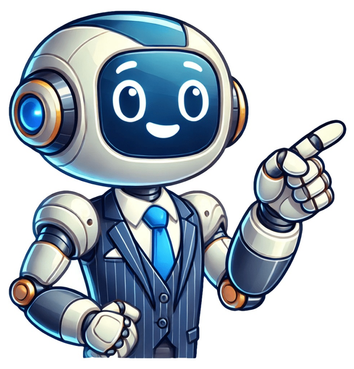

 The role of invasive alien species in the transmission dynamics of zoonotic pathogens is often overlooked, despite the rapid escalation in biological invasions globally. Here we synthesise available information on the influence of invasive alien species on zoonotic pathogen dynamics in invaded ranges, focussing on Europe, and identify key associated knowledge gaps. We identified 272 documented interactions between alien species and zoonotic pathogens within invaded ranges. The majority of these involved invasive alien mammals followed by birds with only a few occurrences of other taxa documented. A wide range of potential interactions between invasive alien species and zoonotic pathogens were identified but few studies considered transmission to humans and so there was limited evidence of actual impacts on human health. However, there is an urgent need to raise awareness of the potential risks posed to human health by the transmission of zoonotic diseases by invasive alien species; the role of invasive alien species in zoonotic disease transmission may exceed that of native wildlife and occur in a relatively short period following the arrival of an invasive alien species within a new region. Ecological and social mechanisms govern the dynamics of zoonotic disease transmission but wildlife diseases are not consistently included within animal, plant and human policies. Rapid advances in the development of systems frameworks that integrate the ecological, economic and social processes promoting spillover in rapidly changing environments will increase understanding to inform decision-making.The online version contains supplementary material available at 10.1007/s10530-022-02978-1.Keywords: Zoonotic pathogens, Invasive non-native species, Disease, Spillover, One healthThe number of alien species arriving in new regions is escalating globally (Seebens et al. 2017) and the interaction of invasivealien species with land use change could be of similar magnitude to the threat of climate change in shifting the distribution of hosts, vectors and reservoirs of pathogens (Hulme 2014). The adverse effects of invasive alien species 1 on biodiversity and ecosystems have been widely documented (Mazza and Tricarico 2018; Pyek et al. 2020). However, the role of alien species in the transmission dynamics of emerging zoonotic diseases2 is often overlooked (Dunn and Hatcher 2015; Hulme, 2017; Roy et al. 2016).Zoonotic diseases make up 60% of emerging infectious disease events worldwide (Jones et al. 2008) and disproportionately affect tropical communities (Halliday et al. 2012) accounting for around one-quarter of Disability Life Adjusted Years lost to infectious diseases in Lower Middle Income Countries (Grace et al. 2012). The impacts of these complex, multi-host pathogens are evolving in response to social-political and environmental change including agricultural intensification, deforestation and climate change (Jones et al. 2008; Plowright et al. 2021). An outcome of ongoing social-political and environmental change is the dramatic shifts and expansion of animal hosts (Johnson et al. 2020) which can increase the probability of contact amongst humans, animal hosts and disease vectors with knock-on consequences for exposure and transmission of zoonotic diseases. For example, abundant and widely distributed species, including those that have expanded their ranges by adapting to human-dominated landscapes, were found to harbour higher loads of zoonotic viruses and pose an increased risk of contributing to human spillover worldwide than those with limited distributions (Johnson et al. 2020). Another global analysis highlighted that disturbed habitats, under substantial human use, harbour a greater richness and total abundance of known wildlife hosts of zoonotic diseases than other habitats (Gibb et al. 2020).Empirical and review studies have highlighted a wide range of mechanisms by which social-ecological and anthropogenic environmental change, including habitat loss, degradation and fragmentation, can alter the interactions between species within a disease transmission network and promote zoonotic disease spillover (Aguirre 2017; Plowright et al. 2021). These have included effects on behaviour, social strucuture and dispersal of species and composition and diversity of communities (Estrada-Pea et al. 2014). Alterations to the composition and diversity of local communities have been shown to increase or decrease zoonotic pathogen transmission. In some cases, new alien species within a community may be suitable hosts for endemic pathogens and so can increase pathogen transmission through spillback to native host species including humans. The connectedness between natural and anthropogenic systems highlights the importance of whole systems approaches to understanding the changing dynamics of pathogens in response to global environmental change (Wood et al. 2012).Panel 1: SARS-CoV-2, mink and the potential for spillback of pathogens to humans and other animalsFollowing an outbreak of SARS-CoV-2 on a farm of American mink, Neogale vison, there was strong evidence to suggest the mink had seemingly contracted the infection from spillover from the human pandemic, at least two farm workers have subsequently caught the virus from the mink (Enserink 2020). In December 2020, a wild American mink in Utah near a fur farm was found to be infected with SARS-CoV-2 representing the first case of a non-captive animal infected with this coronavirus. This is of particularly concern, considering that there are studies demonstrating a clear overlap in habitat use between free-ranging mink populations and farm animals (Hammershj et al. 2005; Valnisty et al. 2020). A further case was reported in Spain with the capture of two American minks in the wild with SARS-CoV-2 infection, although in this case far from fur farms (Aguil-Gisbert et al. 2021). Further study is required to examine the potential risk to other river-roaming species through indirect transmission routes.The extent to which invasive alien speciesare involved in zoonotic disease transmission in changing environments and through which mechanisms has not been well studied although a recent study demonstrated that the number of zoonosis events increase with the richness of alien zoonotic hosts (Zhang et al 2022).It has been hypothesised that invasive alien species may have a disproportionate impact on the transmission of zoonotic pathogens for a number of reasons (Hulme 2014):Alien species may be more effective hosts than other species or vectors in the transmission of endemic pathogens and amplify local pathogens (Chinchio et al. 2020)Alien species may facilitate the establishment of new emerging diseases with which they have co-evolved with in their native range and which may be introduced with them (Dunn and Hatcher 2015)Alien species often thrive in anthropogenic environments so may have high encounter rates with people and often exhibit high dispersal rates including through human-mediated dispersal, with the trade in many alien species being relatively unregulated.The integration of a new host into an established zoonotic network can dramatically increase disease transmission.Here we present a review of the literature on the role of alien species in the emergence and spread of zoonoses recognising the mounting evidence of links between zoonotic diseases and biodiversity change (Johnson et al. 2020; Nuez et al. 2020). A recent analysis highlighted that the introduction of alien species is likely to have contributed to zoonosis emergences in recent history (Zhang et al 2022). Here we assess the extent to which the impacts of invasive alien species on zoonotic disease transmission have already been realised and assessed possible biases in the information available and opportunities for improving our scientific understanding of the role invasive alien species play in zoonotic disease transmission to inform interventions and policy.We conducted a systematic review of published literature following PRISMA guidelines using the Web of Knowledge platform, which includes references from 1960 onwards. All databases within Web of Knowledge were searched, which included Web of Science Core Collection, BIOSIS Citation Index, BIOSIS Previews, KCI Korean Journal Database, MEDLINE, Russian Science Citation Index, SciELO Citation Index (search date: 12th July 2020). We utilised six sets of search strings to retrieve literature (Table 1), which yielded 603 unique references once duplicates were removed. No special operators were used which effectively performs an AND operation between the words in the set. Our search only included papers written in the English language although it should be noted that literature in other languages would undoubtedly have add to the information available.Sets of search strings used to retrieve literature linking zoonotic diseases and invasive alien species and the number of references returned for each setSets of search termsNumber of references returnedAlien species zoonoses48Alien species zoonotic diseases50Invasive species zoonoses262Invasive species zoonotic diseases272Non-native species zoonoses312Non-native species zoonotic diseases290For extraction of data into summary tables, we agreed on inclusion and exclusion criteria which aligned with the scope of the review (Table 2). Full papers were identified following screening of all titles and abstracts, by one of three of the study authors (BVP, ET, HER), and further reviewed as necessary for eligibility and inclusion. Overall, 369 papers out of the 603 were excluded from the study.Inclusion and exclusion criteria used to select studies for the reviewInclusion CriteriaContains primary data on populations of alien species established in the wild outside their native range and causing (or having potential to cause) zoonotic diseaseContains primary data on the role of alien species (or potential role) as a vector or reservoir species for a zoonotic disease in the wild outside their native rangeReviews the role of alien species in zoonotic disease transmission and spread in the wild outside their native range (either considering only the alien species or the alien species in comparison to native species)Contains primary laboratory data on competence of alien species which are vectors or reservoirs for a zoonotic pathogen where the laboratory test populations arefrom outside the native rangeExclusion CriteriaContains only ecological, taxonomic, genetic or physiological data on the alien species with no data on a zoonotic diseaseContains data on alien species involved as a vector or reservoir species for a zoonotic disease in the native range of the IAS only and with no information from outside the native rangeContains data on invasiveness of a pathogen inside host tissue as opposed to data on an alien speciesContains data on a non-invasive scientific method as opposed to data on alien speciesContains data on zoonotic disease in humans without linkage to alien speciesContains data on zoonotic disease links to alien species hosts but the hosts are not identified to speciesContains data on alien species links to zoonotic disease where alien species populations are captive or kept as pets only with no free living alien species populationsContains data on bites by an alien species as health problem rather than infectious zoonotic diseaseReviews that do not explicitly link alien species and zoonotic diseases (e.g. of invasion and biosecurity policy, zoonotic diseases and ecosystems, zoonotic diseases and biogeography, wildlife trade)Data on invasive alien species-zoonotic pathogen interactions from relevant papers was extracted into summary tables (Supplementary Information 1) including taxonomic information (order, family, species) of the invasive alien species and the species or genus name of the pathogen. The role of the invasive alien species in zoonotic disease transmission was classified within broad categories of direct and indirect roles. Direct roles in transmission included being an invasive alien species pathogen of humans, being a reservoir host for a zoonotic pathogen, being an arthropod vector for the zoonotic pathogen (biological or mechanical). Indirect roles included being a host for arthropod vectors of zoonotic pathogens, being a vector for a zoonotic pathogen, or altering vector-hostpathogen dynamics in ways that increase transmission to humans.The type of study was also categorised for each paper. Some of the studies were laboratory-based such as those considering the competence of vectors or reservoirs within the context of zoonoses and others on molecular phylogenetics. Many of the studies were field-based including screening approaches to assess pathogen prevalence within an invasive alien species host through to ecological studies investigating the mechanisms behind zoonotic transmission. There were also a number of biogeographic studies and review papers identified. For each study and where available the following contextual factors were collected: the region and country in which the study took place, the timing of introduction of the alien species and current extent of establishment and spread in the country, information on the status of the zoonotic disease in the study region.To clarify and quantify the extent of impact that invasive alien species are involved in transmission of the parasite or pathogen to humans, we extracted further information on the role of the invasive alien species in the pathways to zoonotic disease transmission (Plowright et al. 2017, 2021) from all the papers identified as relevant (conforming to the inclusion criteria outlined in Table 2).The evidence for each individual invasive alien species and zoonotic pathogen interaction was revisited to evaluate the extent of impact that invasive alien species are having on transmission from a potential impact to an actual (=realised) impact along a continuum (identified by the authors) of available supporting evidence (Table 3). This provided an opportunity to give context to the interaction and specifically some measure of confidence in the extent and magnitude of the impact on humans. Pathogen type and transmission pathways were retrospectively retrieved for pathogens involved in the interactions using a wide range of literature sources (Supplementary Information 2).Continuum of potential and actual impacts of IAS on zoonotic disease spillover with types of supporting evidenceType of impactCertainty of impactType of supporting evidencePotentialVery lowDetection of sporadic pathogen presence or low prevalence (