

*Special Issue: Wildlife Parasitology*

# Parasites and biological invasions: parallels, interactions, and control

Alison M. Dunn<sup>1</sup> and Melanie J. Hatcher<sup>1,2</sup><sup>1</sup> School of Biology, University of Leeds, Leeds LS2 9JT, UK<sup>2</sup> School of Biological Sciences, University of Bristol, Bristol BS8 1TH, UK

**Species distributions are changing at an unprecedented rate owing to human activity. We examine how two key processes of redistribution – biological invasion and disease emergence – are interlinked. There are many parallels between invasion and emergence processes, and invasions can drive the spread of new diseases to wildlife. We examine the potential impacts of invasion and disease emergence, and discuss how these threats can be countered, focusing on biosecurity. In contrast with international policy on emerging diseases of humans and managed species, policy on invasive species and parasites of wildlife is fragmented, and the lack of international cooperation encourages individual parties to minimize their input into control. We call for international policy that acknowledges the strong links between emerging diseases and invasion risk.**

**The changing distribution of hosts and parasites**

Species distributions have always been changing. However, they do so now at an unprecedented rate as a result of human activity leading to habitat change, climate change, biological invasions, and emerging disease. The magnitude of human impact on the biological and physical systems of the Earth has led to the suggestion that we are entering a new geological epoch, the Anthropocene [1,2]. Some of the most dramatic examples of changes in species distribution are biological invasions, the vast majority of which are human-mediated. Invasions are one of the main generators of ecological novelty (Box 1): biological systems (organisms, communities, ecosystems) produced as a result of human activity with few or no historical analogs. Parasites (we use the term to refer collectively to macroparasites, microparasites, and parasitoids) are frequent partners or players in biological invasions because they are either introduced into new communities along with invading species, or are left behind in the ancestral range of the host, affording the host ‘enemy release’. Moreover, parasites are frequently implicated in altering the outcome or impact of invasions, changing the strength of interactions between invasive and native species [3]. Emerging infectious diseases (EIDs) can be considered

to be another class of potentially invasive parasites that spread into new host populations or species [4]. Recent articles recognize the relevance of biological invasions and changing distributions for the spread of zoonoses [5,6]; we consider here the broader implications of invasion for wildlife disease. In this review we focus on the relationship between parasitism and invasion, acknowledging similarities between the processes of invasion and disease emergence [4], and examine the mechanisms by which parasites influence, and are influenced by, invasion, and the consequences of these interactions for species, communities, and ecosystems. We go on to examine the need for new policy, risk analysis, and biosecurity measures to manage or mitigate some of these issues.

**Parasitism and invader-native interactions**

There is often a close link between invasive species (here we define an invasive species as a non-native species that has established in the new range and has spread to form new populations [7]) and parasites. Indeed, parasitic disease of wildlife, managed or human populations is cited as a driver behind the impact of nearly a quarter of species on the IUCN list of the 100 of the World’s Worst Alien Species [4] and fourteen of these involve wildlife diseases: seven of the species listed cause infectious diseases in wildlife, six are reservoirs of parasitic disease that spills over to affect native wildlife, and one is a vector of parasitic disease of wildlife (Table 1). Anthropogenic transport was the route of introduction for the majority of these species.

Invasive parasites can drive changes in host species diversity and abundance, often acting in conjunction with other environmental change. For example, the worldwide amphibian decline is driven by environmental change and ecological novelty including habitat loss, hunting, environmental trade, and the EID chytridiomycosis. This disease is caused by *Batrachochytrium dendrobatidis* (Bd), an invasive fungus (listed in the 100 of the World’s Worst Invasives, Table 1) [8]. The spread of Bd has been linked to several anthropogenic factors including climate change; however, the main driver appears to be the global trade of amphibians that act as reservoirs from which the disease may spill over into wild populations [9–11].

The spread of an invasive species may lead to novel combinations of parasites and hosts. For example, novel parasites co-introduced with an invasive species may spill over into native species. If the native species are more

Corresponding author: Dunn, A.M. (a.dunn@leeds.ac.uk).

Keywords: invasion; emerging infectious disease; wildlife disease; spillover.

1471-4922/

© 2014 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.pt.2014.12.003>

**Box 1. Ecological novelty**

Parasites invading new territories or host species can be considered as 'novel organisms' [67]. Ecological novelty, a concept developed by restoration ecologists, is a term used to describe novel ecological systems with little or no co-evolutionary history and often undergoing rapid ecological or evolutionary change [81]. The realization that many ecological systems are strongly influenced by, and may be inextricable from, human activity has led to the suggestion that we need to understand ecology and evolution in the Anthropocene, and this may require perspectives beyond those of classical ecology in which the influence of humans was largely ignored [82]. The ecological novelty approach accepts the importance of humans in ecology, both in terms of driving chance and as valid players whose socioeconomic needs must also be taken into account.

Ecological novelty can occur at all scales of biological organization. For instance, we can envisage retroviruses integrating into host genomes (e.g., [83]) as novel genetic elements. GMOs, synthetic organisms, and some EIDs constitute novel organisms [67]. Introduced, potentially invasive free-living or parasitic species result in novel communities and ecosystems as a consequence of the biotic and abiotic interactions in which they engage in recipient habitats [67]. An identifying feature of novelty at the ecosystem and landscape scale is a qualitative state-change, where communities have transitioned (owing to fundamental changes in keystone species or resources) such that restoration attempts are unable to regenerate the historical ('reference') state. In such circumstances, acceptance of some degree of transience in ecosystem character, and identification of functionally comparable ecosystems, may provide a more pragmatic and achievable route for restoration or conservation [84,85].

adversely affected, then parasites can be seen as novel weapons used by the invader against the native competitor [12]. For example, squirrel pox virus was co-introduced into the UK with the invasive grey squirrel, *Sciurus carolinensis*. The virus is avirulent to its original host, but spillover leads to high mortality in the native red squirrel *S. vulgaris*, dramatically speeding up its replacement by the invader [13,14]. Similarly, crayfish plague (caused by the fungus *Aphanomyces astaci*) was introduced into Europe by the invasive signal crayfish, *Pacifastacus leniusculus*, and spillover has led to extinction of local populations of the native white clawed crayfish, *Austropotamobius pallipes* [15]. Although parasites can cause local extinctions of novel hosts in the new range, often they rely on the original reservoir host for their persistence. For example, an outbreak of crayfish plague in Ireland, which does not harbor the signal crayfish, led to rapid local decline of the native crayfish, but the fungus then also died out [16]. This potential for burnout of an emerging disease in the absence of the less-affected invasive reservoir can be exploited for conservation. For example, red squirrels can survive in coniferous forest that is unsuitable for grey squirrels. In the UK, conservation of larger red-suitable habitats may enable maintenance of red populations if burnout in the interior red population occurs before reinfection of marginal populations [17].

Invasive species can also influence endemic diseases either by acting as hosts or through their effects on native host species [18]. For example, invasive trout (*Onchorhynchus mykiss* and *Salvelinus fontinalis*) were found to be present at low abundance (3%) in a lake in Argentina. However, they were used as hosts by four endemic parasite species and shed a disproportionate percentage (25%) of parasite eggs [19], potentially leading to a higher infection

risk to native species [18]. Such spillback of parasites from a novel invasive host to the original host can change invasion outcomes. For example, the native leafhopper *Erythroneura elegantula* and the invasive *Erythroneura variabilis* in California are equivalent competitors. However, the invader acts as a reservoir for the native parasitoid *Anagrus epos* which preferentially attacks the native host, shifting the outcome in favor of the invader [20].

Alternatively, if the novel species is a less-competent host for an endemic parasite, then parasite dilution may occur. For example, prevalence of the bacteria *Bartonella birtlesii* and *Bartonella taylorii* in the woodmouse *Apodemus sylvaticus* was found to decline with increasing densities of the invasive bank vole *Myodes glareolus*, which is a less-competent host for the bacteria species [21]. Similarly, in New Zealand, infection intensity of trematodes in native fish decreased with increasing abundance of the invasive brown trout *Salmo trutta* [22].

Conversely, rather than introducing or acquiring parasites, invasive species may lose their parasites in the course of invasion; such 'enemy release' is predicted to enhance competitive ability in the new range [23–25]. This may be particularly important for competitively dominant species that are limited by parasites in their original range, such as plants subject to specialist soil pathogens (plant–soil feedback, discussed below [26,27]). Released from parasitism in the novel range, invading species may be selected to reduce costly defenses in favor of increased resource acquisition and reproductive rates, further enhancing their competitive dominance [28]. Hence, the relationship between parasitism and invasion is unlikely to be static, further complicating the prediction of invasion impacts [29].

In addition to their effect on host survival (population density-mediated effects, as illustrated in the examples above), parasites can also change invasion outcomes through effects on host behavior and life history (trait-mediated effects [30,31]). In Northern Ireland, UK, parasites mediate competition and intraguild predation between native and invasive amphipods. The microsporidium *Pleistophora mulleri* is specific to the native amphipod *Gammarus duebeni celticus* and causes little virulence, but increases the susceptibility of its host to predation by the dominant invader *Gammarus pulex*, while decreasing the ability of the host to prey upon the smaller invaders *Gammarus tigrinus* and *Crangonyx pseudogracilis* [32]. Similarly, the acanthocephalan *Echinorynchus truttae* reduces the predatory impact of the invasive *G. pulex* on the native *G. duebeni celticus* [33], promoting native–invader coexistence. Theory shows that such trait effects of parasites can have as strong an impact on invasion outcomes and coexistence as the more extensively examined density effects [34,35]. Indeed, trait manipulation can be considered as an example of ecological novelty generated by parasites because infected hosts have novel properties that alter their interactions within biological communities.

Parasites thus can mediate native–invader interactions. Similarly, the effects of invaders on native species may influence parasite–host interactions. For example, replacement of the native mud snail, *Cerithidea californica*

**Table 1. Species from the IUCN '100 of the World's Worst Invasive Species' list<sup>a</sup> that either transmit or cause parasitic diseases affecting wildlife**

Species	Impact on wildlife	Mechanism of spread
<b>Invasive parasites</b>		
<i>Aphanomyces astaci</i> (fungus), causes crayfish plague	Spillover of <i>Aphanomyces astaci</i> from invasive signal crayfish (introduced for aquaculture and became invasive) to native white clawed crayfish has led to local population extinctions and widespread decline of the endangered native species (which is also harvested for food) across Europe	Parasite co-introduced with the farmed host which subsequently became invasive
<i>Batrachochytrium dendrobatidis</i> (fungus), causes chytrid disease	An emerging infectious disease and a key driver of amphibian declines. Spread is attributed to multiple factors including climate change and spillover from the invasive American bullfrog	Widespread introduction with the farmed reservoir host which subsequently became invasive
<i>Cryphonectria parasitica</i> (fungus), causes chestnut blight	Chestnut blight led to mass die-off of chestnuts and consequent community-wide changes	Introduced by nursery trade from Japan to North America  Local spread by windborne spores
<i>Ophiostoma ulmi</i> (fungus), causes Dutch elm disease	Spillover of Dutch elm disease into elm caused mass die-off of this dominant overstorey species in Europe with community-wide effects	Introduced (probably from Asia) into America, Europe, and New Zealand, likely by timber trade  Locally transmitted by horticulture/farming and wildlife (bark beetles)
<i>Phytophthora cinnamomi</i> , cinnamon fungus	Declines in native woody perennials some of which are endangered  Declines in forestry and fruit production	Introduced into Europe, North America, and Australasia from Asia via agriculture, forestry and the nursery trade  Locally spread by spore dispersal.
<i>Plasmodium relictum</i> (protist), causes avian malaria	Avian malaria was a key factor in the extinction of approximately half of the endemic bird species in Hawaii	Bird introductions from Africa co-introduced malaria into Hawaii, Europe, and North America
<i>Morbillivirus</i> , causes rinderpest	Transmission from domestic cattle led to declines in wild ungulates. The disease also caused loss of farmed cattle and famine	Spillover from farmed cattle (high densities enabled disease persistence) to wild ungulates Eradicated in 2010 as a result of a global vaccination program
<b>Invasive species that are reservoirs for parasitic disease</b>		
<i>Oncorhynchus mykiss</i> , rainbow trout	Rainbow trout is a reservoir for <i>Myxobolus cerebralis</i> which causes outbreaks of whirling disease in wild fish <sup>b</sup>	Reservoir host introduced into multiple countries for sport and aquaculture farming
<i>Sciurus carolinensis</i> , grey squirrel	Competitive replacement of red squirrel <i>Sciurus vulgaris</i> by the invader is mediated by the squirrel pox virus. The grey squirrel is a reservoir for the virus	Grey squirrels introduced from North America into Europe harbored the virus
<i>Lithobates catesbeianus</i> ( <i>Rana catesbeiana</i> ), American bullfrog	The bullfrog is a reservoir for chytrid disease ( <i>Batrachochytrium dendrobatidis</i> , also listed, see above), which has caused widespread amphibian declines	The bullfrog has been introduced into numerous countries for food and for predatory biocontrol of insects  The bullfrog harbors chytrid disease ( <i>Batrachochytrium dendrobatidis</i> )
<i>Sturnus vulgaris</i> , starling	Reservoir for diseases including <i>Plasmodium relictum</i> (this parasite is itself on the WW list) and <i>Chlamydophila psittaci</i> which causes psittacosis and can infect humans	The starling has been introduced worldwide from its native range in Africa, Asia, and Europe, and is a reservoir for avian and human diseases
<i>Gambusia affinis</i> , mosquito fish	Mosquito fish may act as a reservoir for helminths <sup>b</sup>	Native to North America and introduced into many regions as predatory biocontrol for mosquitoes
<i>Herpestes auropunctatus</i> , small Indian mongoose	The mongoose is a reservoir for parasites of wildlife <i>Lyssavirus</i> (rabies) <sup>b</sup>	Introduced into South America and several islands as predatory biocontrol for rats and snakes
<b>Invasive vector of parasitic disease</b>		
<i>Anopheles quadrimaculatus</i> , mosquito	Vector for malaria ( <i>Plasmodium falciparum</i> , <i>Plasmodium vivax</i> , and <i>Plasmodium malariae</i> ) and for West Nile virus in the USA	Native to North America, linked to disease outbreaks in America

<sup>a</sup><http://www.issg.org/database/species/search.asp?st=100ss><sup>b</sup>The main impact of invasion is through the predatory or competitive impact of the invader on native species, with disease transmission cited as a secondary factor.

by the invasive *Batillaria cumingi* in California led to a reduction in trematode diversity [36], while the invasive trout (*Salmo truttae*) has driven a habitat shift (a trait-mediated effect) by native *Galaxias* fish, which may increase their exposure to trematode parasites [18].

Replacement of native perennial bunchgrasses in California by annual invasive grasses is driven by

parasite-mediated competition. Uninfected bunchgrasses outcompete the invasive species. However, the invasive grasses amplify the aphid vector for Barley and cereal yellow dwarf viruses (BYDV) which cause both stunting (a trait effect) and mortality (density) in the native grasses, making gaps available for establishment of the invaders [37]. Endophytes (obligate endosymbionts,

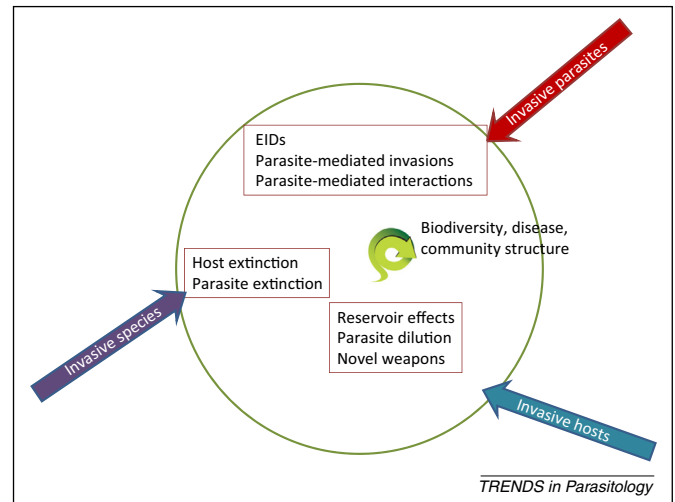


often with beneficial effects on their host) are also implicated in the invasive success of some annual grasses [38]. Plant–soil feedback (the accumulation over time of below-ground species-specific parasites and symbionts) may also be associated with invasion success [26], and may explain large-scale altitudinal and latitudinal patterns of invasion and diversity [39].

### Ecosystem-level consequences of invading parasites

Many parasites that invade with their hosts have community or ecosystem-level consequences, contributing to ecological novelty at the ecosystem or landscape scale [3,40]. For instance, in the example above, parasite-mediated replacement of native amphipods by the invasive *G. pulex* does not represent a functionally analogous swap, but has led to communities with lower invertebrate diversity and abundance with potential higher-order effects on fish predators [41]. Parasites of plants are reported to have knock-on effects at higher trophic levels. For example, endophytes (*Neotyphodium* spp.) of the invasive grass *Lolium arundinaceum* promote alkaloid production in the host, reducing nutritional quality and palatability; this can shift herbivore pressure from the host onto competing native grasses, influencing invasion success but also indirectly affecting detritivore and predator (spider) communities [42,43]. Parasites that are most detrimental to competitively dominant host species enhance biodiversity [44,45], whereas those with greater deleterious effects on weaker competitors are predicted to reduce species coexistence [35,46]. Shared parasites may also influence coexistence outcomes, even if the host species do not interact directly, via apparent competition [46–48]. Parasites also influence predator–prey and herbivore–plant interactions via trait or density-mediated indirect effects [3,31]. Indeed, wildlife EIDs are responsible for some of the most dramatic biotically driven landscape change in recent history (e.g., American chestnut blight, Dutch elm disease, myxomatosis, rinderpest; reviewed in [29]). By contrast, restoration ecologists utilize some parasites to enhance biodiversity (e.g., yellow rattle, *Rhinanthus* spp., is used in grassland restoration [49]) or to provide additional habitats and resources (e.g., mistletoes [50]). More generally, parasites may play key roles in ecosystem function [51] and are important components of biological diversity [52]. An important advance is the realization that parasites can dramatically alter the characteristics of food webs [53,54]. For instance, the free-living stages of parasites are prey for a variety of species, influencing parasite prevalence [55] and cementing trophic links in food webs [56,57]. Furthermore, parasites influence the types of interactions that are most commonly observed in ecological networks (increasing the relative frequency of apparent competition and intraguild predation motifs [58]). These effects can influence community stability (i.e., robustness to extinction and resilience to perturbation [59–61]). These may be important factors to consider when predicting the impact on wildlife of invading or emerging parasites (Figure 1) [62,63].

Many parasites infect multiple host species, and here parasite prevalence depends on community composition, which influences contact and transmission rates between viable hosts. However, as we have seen, parasites can also



**Figure 1.** Alternative ways in which invaders cause ecological novelty through their interactions with parasites. Green circle: native community. Red arrow: invasive parasites can drive changes in host abundance and extinction and can mediate native/invaser interactions, leading to changes in biodiversity and community structure. Blue arrow: invasive hosts can co-introduce parasites which may act as novel weapons; invasive species may also acquire endemic parasites resulting in parasite amplification or dilution. Purple arrow: extinctions and changes in community structure as a result of biological invasions can affect native parasite–host interactions. Green spiral: feedback between parasite prevalence and biodiversity. Abbreviations: EIDs, emerging infectious diseases.

influence community composition; hence, the relationship between disease emergence and biodiversity is complex (and controversial, Box 2). Again, this relationship is dynamic, and predicting the consequences of invading parasites is therefore difficult and is likely to require case-specific examination. Because feedback between parasite prevalence and biodiversity can potentially lead to new community configurations [40], as with restoration ecology, we may have to accept irreversible change in some ecosystems subject to invading parasites or their hosts.

### Invasion/emergence processes and management

With increasing economic development, global trade, and transport, the opportunities for translocating species with the potential to spread disease are increasing [64,65]. Prevention or management requires an understanding of the processes leading to disease emergence and invasion because control approaches are stage-dependent. Disease emergence follows a similar progression of stages to invasion (Figure 2), in part because some are caused by range-expanding parasites or those brought along by invading hosts. With appropriate adjustments of organizational scale, similarities also exist between EIDs arising via spill-over to novel host species [4,66]; these frameworks can be extended further to novelty at other ecological scales [67].

The management framework for invasions/emerging diseases can be summarized in terms of prevention (of translocation and introduction), containment or eradication (upon introduction to prevent establishment), and mitigation (to limit further invasive spread [7]). Prevention includes biosecurity measures (Box 3) and early-warning practices including horizon scanning, surveillance and risk assessment. Containment strategies also involve surveillance and monitoring, coupled with active intervention to eradicate or limit the spread of established

### Box 2. Biodiversity and disease emergence

The relationship between parasite prevalence and biodiversity is bidirectional, with the potential for each to feed back on the other [40]. Parasitism can influence biodiversity, promoting or inhibiting host species coexistence through many processes, including direct (mortality) effects on hosts, apparent competition [47], parasite-mediated competition [46,48], and parasite–predator interactions [31]. However, biodiversity can also influence disease dynamics, potentially increasing or decreasing parasite establishment and prevalence [86].

A growing list of examples, including Lyme disease, West Nile virus, hantavirus, and foliar fungal pathogens, show evidence that more diverse communities exhibit lower parasite prevalence and consequently impart lower disease ‘risk’ (from the perspective of key host species; reviewed in [86]). This has led to rancorous debate because counter-examples can also be cited ([87], but see [88]), and patterns may be scale-dependent ([89,90], but see [91]). However, the earlier papers in this field (both theoretical and empirical) were very clear that the relationship (if any) between biodiversity and parasite establishment was context- and process-dependent, and could go either way. Whether biodiversity increases or decreases parasite establishment depends on the mode of transmission (frequency- or density-dependence [92]) and on community composition (in particular, the relative frequency of competent versus non-competent hosts in the community [93]). Competent host frequency may increase, decrease, or be unrelated to biodiversity. If more-diverse communities contain a higher frequency of less-competent hosts, a dilution effect is produced, reducing effective transmission and consequently buffering against disease risk. Different processes may lead to dilution effects, including diversity-enhanced physical separation between hosts [94], ‘wasted bites’ on non-competent hosts for vector-borne diseases [95], and within-host parasite interactions [96]. Other factors correlated with biodiversity (e.g., trait-mediated or trophic impacts of predators, or changes in encounter/transmission opportunities with forestation [86,90]) may override these processes, complicating or reversing disease risk relationships with biodiversity.

populations. If novel hosts or parasites do become established, strategies focus on mitigation of their impact or the prevention of further spread, again involving biosecurity and population management. It is widely accepted that action taken at early stages of invasion or emergence – such as preventative biosecurity measures – are more cost-effective and more likely to succeed than are the options for control or mitigation that are available at later stages of the process [4,68].

### Policy to control invasive species and emerging diseases

International policy to control the spread of new and re-emerging human and animal diseases is led by the World Health Organization (WHO) and the World Organization for Animal Health (OIE, the acronym is retained from the original Office International des Epizooties), respectively. The International Health Regulations ([http://www.who.int/topics/international\\_health\\_regulations/en/](http://www.who.int/topics/international_health_regulations/en/)) require the WHO 196 member countries to report disease outbreaks and risks due to the movement of people or disease vectors; in the event of a disease outbreak the WHO Global Outbreak Alert and Response Network acts to enable rapid disease identification and responses, as in the current Ebola outbreak in Africa (<http://www.who.int/csr/outbreaknetwork/en/>).

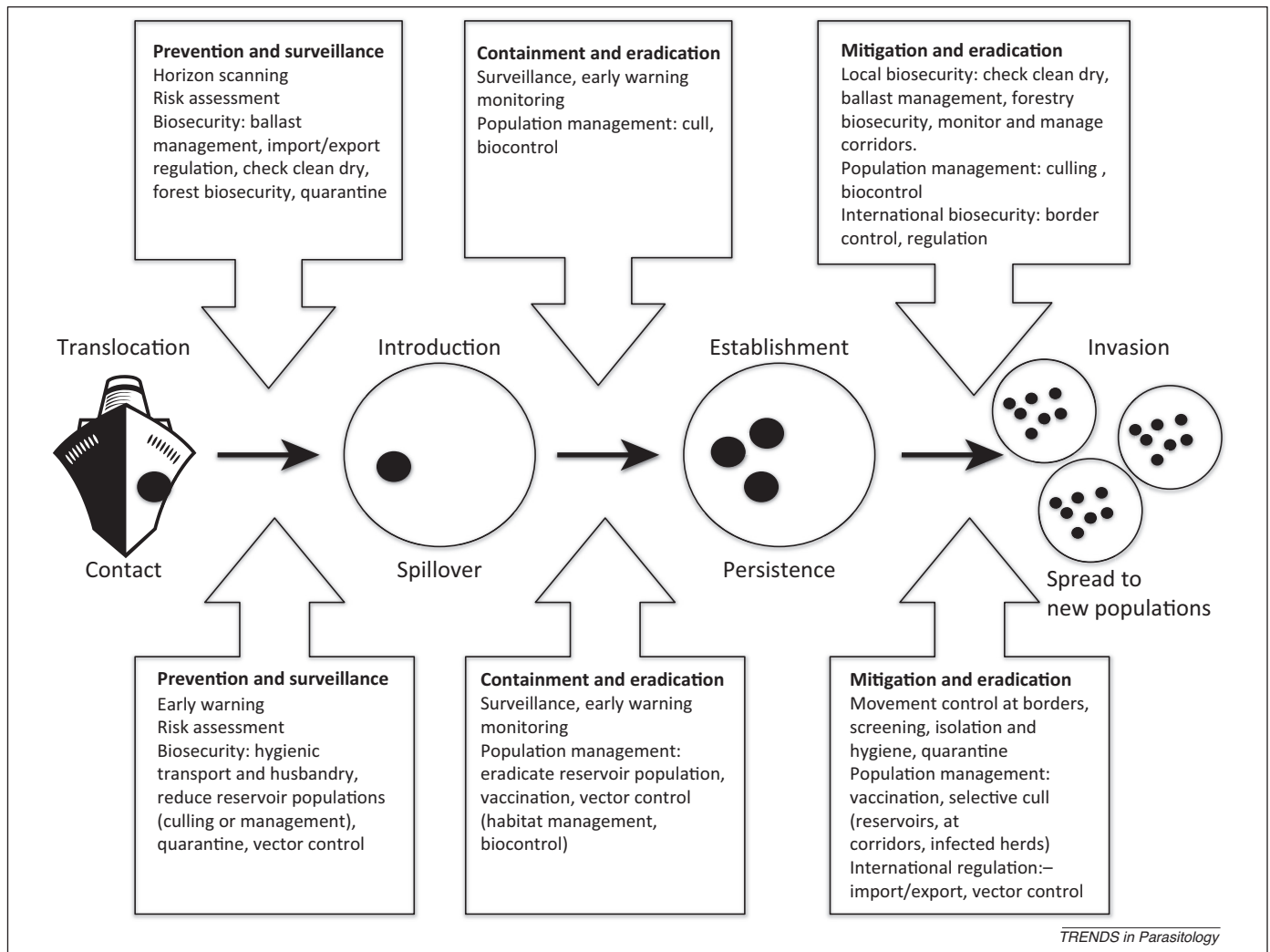
The OIE Terrestrial Animal Health Code (<http://www.oie.int/en/international-standard-setting/terrestrial-code/>)

and Aquatic Animal Health Code (<http://www.oie.int/en/international-standard-setting/aquatic-code/>) set standards to ensure the sanitary safety of international trade in animals and their products. The 178 member countries are required to provide notification of listed or emerging animal diseases and of measures taken to prevent disease spread. These animal health codes are recognized by the World Trade Organization (WTO). However, unlike the WHO, the role of the OIE is limited to providing individual countries with information to enable them respond to animal diseases [69].

In contrast with international policy on EIDs of humans and managed animals and plants, other invasive species and parasites of wildlife (that do not have direct human medical or economic impact) fall between the gaps of many regulatory bodies. Under the WTO Agreement of the Application of Sanitary and Phytosanitary Measures (SPS, [http://www.wto.org/english/res\\_e/booksp\\_e/agrmntseries4\\_sps\\_e.pdf](http://www.wto.org/english/res_e/booksp_e/agrmntseries4_sps_e.pdf)), and the General Agreement on Tariffs and Trade (GATT), individual countries can restrict trade to protect animal or plant health or food safety. The International Plant Protection Convention (IPPC; <https://www.ippc.int/about/convention-text>) is recognized by the WTO and aims to secure action to prevent and to control the introduction and spread of pest organisms including weeds and invasive species, of plants, plant products, and wild plants. However, because the SPS and IPPC focus mainly on traded and farmed animals and plants, they are likely to miss many invasive species and parasites that affect wildlife. The environmental impact of such species and their indirect economic or medical impacts may nevertheless be substantial [6]. Such invaders [62], often transported (intentionally or unintentionally) via trade or transport, result in the costs of biosecurity or eradication being borne by the public purse in recipient countries. Without enforced legislation to internalize the costs of biosecurity, there is no economic incentive for commerce to take appropriate measures. International cooperation over biosecurity legislation is hampered by the prisoner’s dilemma (a game theory showing that cooperators lose out to defectors) nature of this interaction. Furthermore, the SPS aims to prevent countries from implementing protectionist trade barriers [68]; indeed, under GATT countries are not permitted to cooperate to use trade restrictions to limit pest or pathogen transmission except in cases of emerging human diseases [62].

Invasive species are specifically included in the UN Convention on Biodiversity Aichi Biodiversity Targets: ‘By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment’ (<http://www.cbd.int/sp/targets/>). However, legislation to control the spread of invasive species tends to be at national levels or indeed absent.

One exception to the lack of international legislation is The Ballast Water Management Convention ([http://www.imo.org/About/Conventions/ListOfConventions/Pages/International-Convention-for-the-Control-and-Management-of-Ships'-Ballast-Water-and-Sediments-\(BWM\).aspx](http://www.imo.org/About/Conventions/ListOfConventions/Pages/International-Convention-for-the-Control-and-Management-of-Ships'-Ballast-Water-and-Sediments-(BWM).aspx)). However, although adopted in 2004, the



**Figure 2.** Parallel processes of biological invasion and disease emergence, depicting stage-specific control strategies. Four stages are commonly distinguished (some models include further substages), termed translocation (for invaders) or contact (for emerging infectious diseases, EIDs, particularly those emerging in novel host species [97]); introduction into the novel/recipient habitat (or spillover for novel host EIDs); establishment or persistence (once invader/parasite populations are self-sustaining in the novel habitat), and invasive spread (for invaders, populations that undergo local range expansion and cause substantial impact in the recipient habitat, or are transported over a wide geographic area; for EIDs, case reports from a broad geographic range or indicating spread to distinct populations). Open circles represent recipient habitat/host; filled circles represent invader/parasite. For discussion of control strategies, see text.

convention has not been ratified by several key maritime countries, limiting its effectiveness.

The most effective current invasive-species legislation tends to be at national levels, perhaps because of the lack of incentive for co-operation at international levels. Australia and New Zealand are recognized as being at the forefront of invasive species management [70]. The Australian Weed Risk Assessment (WRA; <http://www.daff.gov.au/ba/reviews/weeds/system>) requires risk assessment of all new plant species before introduction into the country, and exclusion of high-risk species; similar legislation is in place in New Zealand. The Australian 1999 Environment Protection and Biodiversity Conservation Act (<http://www.environment.gov.au/epbc>) identifies invasive species as key threats to native species and ecological communities, with environmental, animal, and plant biosecurity being managed by the National Biosecurity Committee. The 1993 New Zealand Biosecurity legislation (<http://www.legislation.govt.nz/act/public/1993/0095/latest/DLM314623.html>) covers pests and unwanted organisms

capable of causing harm to the economy, environment, or public health and has three aims: prevention and exclusion of pests and unwanted organisms, surveillance and response, and management of established pests and unwanted organisms.

More than 20 years later, the EU is putting into place Invasive Alien Species legislation that will identify high-risk invasive species and, paralleling the New Zealand aims, will require member states to put into place prevention, early warning, and management/mitigation of invasive species (EC 2014: <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52013PC0620>). It is crucial that parasites of humans, managed populations, and wildlife are given careful consideration when drawing up the proposed list of species of concern to member countries.

### Risk analysis

Central to management of both EIDs and invasive species are risk assessments enabling us to identify high-risk

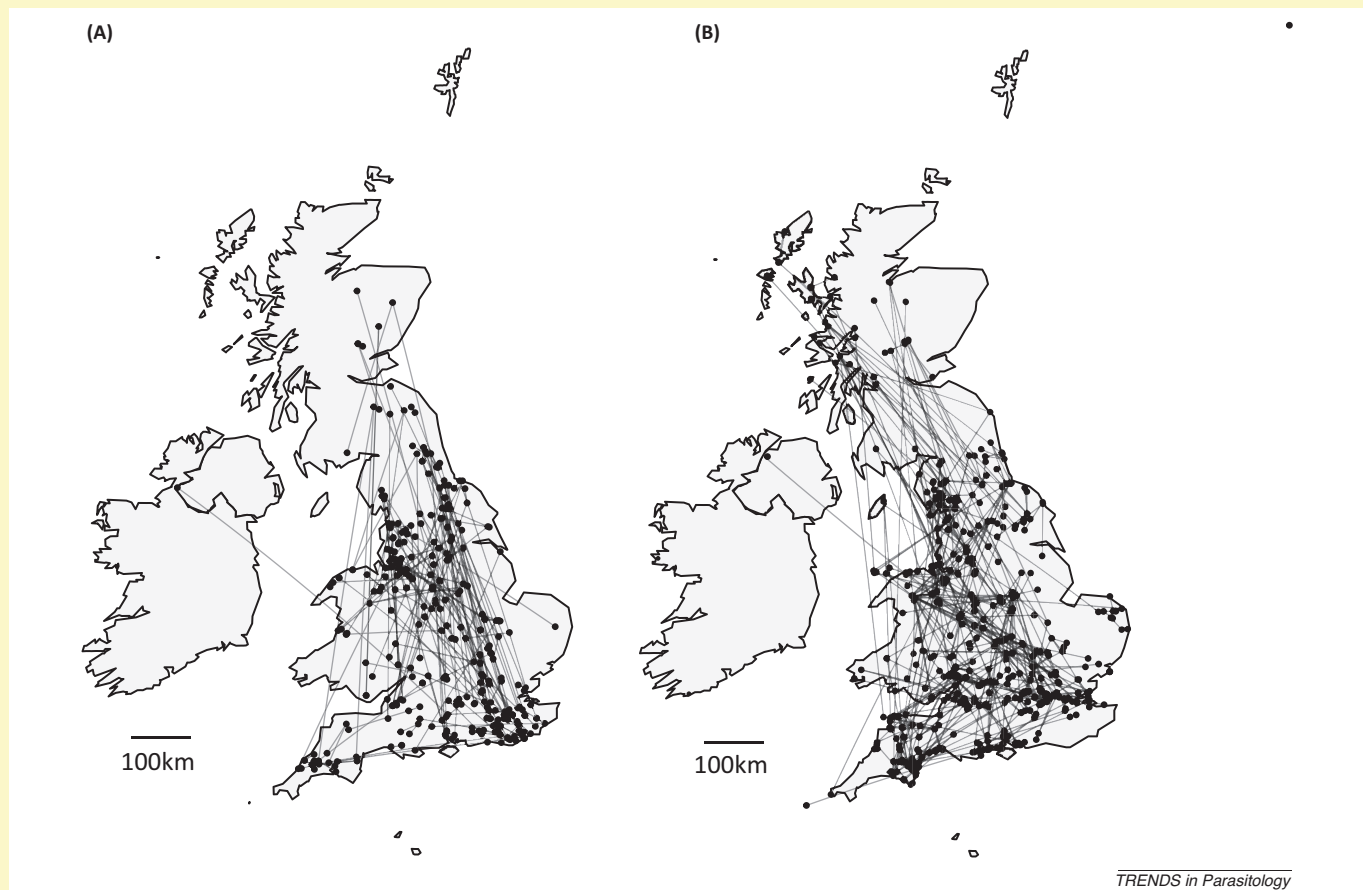
### Box 3. Biosecurity

Increasing global travel and trade provide unprecedented opportunities for the spread of diseases of humans, farmed populations, and wildlife [29] and for the spread of invasive species [68]. Biosecurity, the 'protection against the incursion or escape of potentially harmful or undesirable organisms' [98], is the first line of defense against invasive species and emerging diseases. Monitoring potential introduction pathways increases the likelihood of detecting harmful species and is central to international policy to control disease spread as well as the IUCN Aichi biodiversity targets to control invasive species. However, general biosecurity practice is also crucial in removing potentially harmful species, and can be embedded into the general activities of trade, travel, and recreation without requiring specialist knowledge of harmful organisms. For example, ballast water is a vector for invasive species and pathogens of plants and animals including humans. Ballast water exchange kills these 'hitch-hikers', reducing introduction probability in marine and freshwater [99,100]. Similarly, forestry biosecurity involves the cleaning of vehicles, footwear, and equipment before leaving a site to limit the transfer of invasive plants and plant pathogens (e.g., <http://www.forestry.gov.uk/forestry/infid-8zjmq4>). These practices are relatively low-cost and simple to put in place. However, their effectiveness relies on the widespread engagement of environment practitioners, businesses, and the public, as well as on changes in human behavior.

#### Case study: biosecurity in freshwaters

Freshwaters are vulnerable to the introduction of invasive species and EIDs as a result of the multiple pathways for intentional or unintentional introductions [101]. A campaign launched in New Zealand in 2005 to encourage water users to check their equipment for 'hitch-hikers' and to clean and dry it to kill any organisms has been highly successful in raising awareness and slowing the spread of the invasive diatom *Didymosphenia geminata* (didymo [102]). A similar campaign was launched in the UK in 2010 (<http://www.nonnativespecies.org/checkcleandry/index.cfm?>). However, current awareness and compliance is low, and a survey of recreational water users revealed that a high percentage of anglers (64%) and canoeists (78%) used their equipment/boat in more than one catchment within a fortnight (Figure 1) [103]. Because many aquatic invaders and parasites can survive for several days in damp environments, this represents a biosecurity risk.

The UK Check Clean Dry campaign does not recommend any specific cleaning method to kill potential hitch-hikers. Biosecurity measures for parasitic diseases of fish include chemical disinfection of equipment (e.g., <http://www.nonnativespecies.org/index.cfm?pageid=174>). However, to increase compliance among the public and recreational water users, there is need for simple effective biosecurity measures. A recent study demonstrated the effectiveness of hand-hot water (45°C for 15 minutes) as a simple and safe method that causes rapid mortality of invasive plants and animals ([104]; <http://www.nonnativespecies.org/news/index.cfm>) although its effectiveness in killing parasites remains to be tested.



**Figure 1.** Patterns of movement by recreational water users indicate the potential for translocation of invasive species and diseases (from [103]). UK Maps showing the most recent three sites visited by (A) anglers and (B) canoeists who visited more than one catchment within a fortnight and who did not clean or dry their equipment between use. Lines connect sites (points) visited by an individual within a fortnight.

scenarios and to target resources accordingly. Environmental risk assessment is a standard tool for examining likely consequences of cultivation/husbandry, release, or movement of organisms, including parasites, pathogens or

parasitoids [71]. Risk can in principle be quantified: it is the probability of an event (or hazard) occurring multiplied by a function of the impact (the consequences or damage) of that event (the appropriate functions are a subject of



debate [72]). One of the main hazards for organisms imported or released (e.g., for biocontrol) is the possibility that they (or the parasites/pathogens associated with them) establish in the recipient environment and potentially become invasive. For example, the harlequin ladybird was released for biocontrol and has subsequently become invasive [73]; trade in timber led to the spread of diseases including Dutch elm disease and chestnut blight to native populations [74].

The format for ERAs broadly follows a tiered approach (reviewed in [75]) involving (i) problem formulation (broad consideration of the potential hazards), (ii) hazard characterization (quantifying their impact), and (iii) exposure characterization (quantifying likelihood of a given hazard occurring); (iv) risk characterization (combining measures from (ii) and (iii) to evaluate risk), (v) risk management (considering monitoring, control and mitigation strategies), and (vi) overall risk evaluation (in which the impact of monitoring and mitigation strategies on hazard is also considered; cost-benefit arguments may also be employed). Similar formats are used for deliberate introductions/releases (e.g., biocontrol agents [71]) and genetically modified organisms (EC, 2001: <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32001L0018> [75]). Risk assessment for alien invasive species broadly follows similar patterns [76] but, because these arrive as unintentional introductions, additional preliminary stages are necessary to identify potentially threatening species. Quantitative modeling and qualitative (ranking) approaches have been employed, with the former often focusing on establishment processes, and the latter on impact [72]. Horizon scanning, a broadly qualitative approach for rapid evaluation (combining expert opinion, consensus methods, and data/literature search), may be particularly relevant for upcoming legislation and early warning [77]. For instance, legislature currently under consideration by the EU to prevent biological invasions focuses on biosecurity (with border control of a designated list of hazardous species) and monitoring to allow early detection and implementation of eradication programs (EC 2014: <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52013PC0620>). As part of the cost-benefit analysis undertaken when drawing up the legislation, more stringent measures, such as obligatory application for permits to release any species of concern to any Member state, were ruled out (EC, 2014: <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52013PC0620>).

Reliable risk assessment requires accurate quantification, and this is often problematic where risks of invasion are concerned because the likelihood of establishment and spread depends on numerous biotic and abiotic interactions. Furthermore, quantifying the costs/consequences (e.g., of invasion) will depend on the spatial and temporal scale over which they are considered. In addition, issues involving public perception can make risk assessment problematic. The words 'risk' and 'hazard' have negative connotations that cloud judgment as to the extent of potential harm [78]. Indeed, if all change is regarded as harmful, any human intervention, despite its potential socioeconomic benefits, may be regarded as being 'too risky' – as reflected in current public opinion across many

#### Box 4. Psychology of Risk

##### *Fear of the unknown*

Psychometric testing of public perception of risk demonstrates that people tend to regard particularly frightening hazards (such as nuclear power-plant explosion) and unseen, unknown or uncontrollable events (e.g., chemical contamination, EIDs) as possessing higher degrees of unacceptable risk; these two axes have been characterized as representing 'dread' and 'uncertainty' [105]. These and other psychological biases can lead to large disparities between expert and lay estimates of risk, exacerbated by signal reinforcement (perceived 'risky' activities, such as the cultivation or consumption of GMOs, receive greater media coverage, thereby enhancing perceived levels of risk). Unfortunately, ecological risks such as biodiversity and habitat loss, although evoking strong emotions, are not perceived in terms of 'dread' [106], potentially leading to relative under-estimation of risk. Risk perception can also be inversely related to perceived human benefit; activities that people enjoy, such as tourism and collecting wilderness souvenirs, were on average ranked as posing little or no risk to the environment, despite their potential for species translocation [106]. Similarly, a recent study revealed that public awareness of invasive species was not correlated with the ecological risks they posed, but was influenced by tangible effects on people (such as impacts on recreation or a food source), charismatic species, and media coverage [107].

##### *Framing*

Human attitudes to risk and value were examined through a survey of university students and staff [108]. In this study, the importance of question-framing (in terms of loss or gain) was illustrated by a hypothetical disease-outbreak scenario in which the expected loss (without a control strategy) was stated as 600 lives. Most (72%) of the 152 undergraduates asked chose a control strategy that would lead to 200 lives being saved with certainty; only 28% chose the alternative offered (a 1/3 chance of saving all 600 lives and 2/3 chance of all 600 dying), even though the two strategies have the same expected payoff. By contrast, when the same problem was posed to a different group of students, but the control strategies were framed in terms of loss, the majority chose the probabilistic scenario (78% chose a strategy yielding 1/3 probability that nobody will die, 2/3 probability that 600 would die, compared to 22% opting for a strategy resulting in 400 fatalities). Again, these scenarios, identical apart from framing to the previous pair, had the same average payoff; suggesting that people are prepared to accept more risk to avoid potential losses than to achieve potential gain.

EU states concerning genetically modified organisms (GMOs). Furthermore, perception of risk depends strongly on prior experience of perceived hazards: GMOs and EIDs, of which society has little experience, rank highly in terms of 'dread' and perceived risk (Box 4). A more-nuanced approach, recognizing the inevitability of some degree of environmental change, is apparent in currently shifting paradigms in restoration ecology concerning the management of ecological novelty (Box 1).

#### Risk management

How problems are framed can strongly influence the perception of risk and hazard, and the actions deemed appropriate for mitigation. Psychological tests show that people behave irrationally where risk is concerned, and tend to be risk-averse when problems are framed in terms of potential gains, and risk-taking when the potential for loss is emphasized (Box 4). Hence, public consultations or participation in biosecurity measures, for instance on matters of disease or invasion risk, will need to consider carefully how problems are framed, especially in relation to financial or personal costs of alternative strategies. Cooperation between trading partners can also be difficult to achieve without strict regulation and policing. Countries may take



a defensive approach to border control for imports because they reap the benefits of biosecurity directly. By contrast, the cost of export biosecurity measures is born by the originating country alone, while the benefits accrue to all countries in receipt of the exports [62].

### Concluding remarks

We have focused on invasions and diseases of wildlife. However, control of invasions and of wildlife diseases is also important for human health. Indeed, the majority of human EIDs are zoonoses, most of which originated in wildlife [65]. Biological invasions lead to novel parasite–host interactions and transmission opportunities, with the potential to affect human, wildlife, and ecosystem health and resilience (the ‘One Health’ triad [79]). It is therefore clear that control of invasions and wildlife diseases is also important to limit the risk of human zoonotic EIDs [6].

There are many parallels in the strategies needed to control the spread of EIDs and invasive species, and these are reflected in policy and legislation. Common to both EID and invasive species policy is the importance of biosecurity precautions to prevent the introduction or spread of these species. It is recognized that preventing the introduction of an invasive alien species is more cost-effective than attempting to eradicate or even mitigate the effect of established invaders [68]. This is reflected in the Australian, New Zealand, and impending EU legislation which focus on prevention and exclusion. Given the current realization of the interplay between invasions and diseases, it is important that this legislation considers parasitic diseases as well as the more traditional invaders. Similarly, focus on surveillance and monitoring of human EIDs is the most effective way to minimize health and economic costs. However, despite being identified as a key risk to food security and the natural environment (<http://www.issg.org/pdf/riopolicybrief.pdf>), legislation to control invasive species lags behind that for EIDs with regard to enforcement power and international cooperation. Furthermore, the lack of international cooperation on invasive species results in a prisoner’s dilemma scenario whereby it pays individual parties to focus on import biosecurity at the expense of that for exports [62]. International cooperation is vital because the rates of intentional and unintentional species translocations are unprecedented.

Despite biosecurity and surveillance measures, some biological invasions and EIDs will succeed; indeed, invasion and disease emergence have been a force throughout evolutionary and ecological history. Under such circumstances we have options to mitigate or eradicate; the economic cost of which must be weighed against the socio-economic and ecological benefits. Some control options may be too costly or could exacerbate situations in the longer term (compare the short- and long-term implications of antibiotic usage with regard to the evolution of virulence [80]). Furthermore, as with ecological restoration, eradication programs are not always successful, and return to the pre-invasion state may not be feasible. It thus seems inevitable that we will be obliged to accept a degree of novelty in our ecosystems, including novel hosts and parasites. Recent perspectives on restoration, accepting the transient nature of systems and identifying functionally

analogous equivalents, should now be explored by invasion ecologists and parasitologists.

### Acknowledgments

This work was funded by National Environmental Research Council (NERC) grant NE/L01274X and by a NERC/University of Leeds Impact Accelerator Award. We thank Chris Tofts, Jaimie Dick, Lucy Anderson, and Anita Glover for stimulating discussions, and Jonathan Jeschke and Cara Nelson for insights into ecological novelty and restoration.

### References

- 1 Steffen, W. *et al.* (2011) The Anthropocene: conceptual and historical perspectives. *Philos. Transact. A. Math. Phys. Eng. Sci.* 369, 842–867
- 2 Kueffer, C. and Kaiser-Bunbury, C.N. (2013) Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. *Front. Ecol. Environ.* 12, 131–137
- 3 Dunn, A.M. *et al.* (2012) Indirect effects of parasites in invasions. *Funct. Ecol.* 26, 1262–1274
- 4 Hatcher, M.J. *et al.* (2012) Disease emergence and invasions. *Funct. Ecol.* 26, 1275–1287
- 5 Estrada-Pena, A. *et al.* (2014) Effects of environmental change on zoonotic disease risk: an ecological primer. *Trends Parasitol.* 30, 205–214
- 6 Hulme, P.E. (2014) Invasive species challenge the global response to emerging diseases. *Trends Parasitol.* 30, 267–270
- 7 Blackburn, T.M. *et al.* (2011) A proposed unified framework for biological invasions. *Trends Ecol. Evol.* 26, 333–339
- 8 Crawford, A.J. *et al.* (2010) Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proc. Natl. Acad. Sci. U.S.A.* 107, 13777–13782
- 9 Voyles, J. *et al.* (2012) Temperature alters reproductive life history patterns in *Batrachochytrium dendrobatidis*, a lethal pathogen associated with the global loss of amphibians. *Ecol. Evol.* 2, 2241–2249
- 10 Lips, K.R. *et al.* (2008) Riding the wave: Reconciling the roles of disease and climate change in amphibian declines. *PLoS Biol.* 6, 441–454
- 11 Fisher, M.C. *et al.* (2012) Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484, 186–194
- 12 Price, P.W. *et al.* (1986) Parasite mediation in ecological interactions. *Annu. Rev. Ecol. Syst.* 17, 487–505
- 13 Tompkins, D.M. *et al.* (2003) Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecol. Lett.* 6, 189–196
- 14 Strauss, A. *et al.* (2012) Invading with biological weapons: the importance of disease-mediated invasions. *Funct. Ecol.* 26, 1249–1261
- 15 Holdich, D.M. and Poeckl, M. (2007) Invasive crustaceans in European inland waters. In *Biological Invaders in Inland Waters: Profiles, Distribution and Threats* (Gherardi, F., ed.), pp. 29–75, Springer
- 16 Reynolds, J.D. (1988) Crayfish extinctions and crayfish plague in central Ireland. *Biol. Conserv.* 45, 279–285
- 17 Gurnell, J. *et al.* (2006) Squirrel poxvirus: landscape scale strategies for managing disease threat. *Biol. Conserv.* 131, 287–295
- 18 Poulin, R. *et al.* (2011) Biological invasions and the dynamics of endemic diseases in freshwater ecosystems. *Freshwater Biol.* 56, 676–688
- 19 Rauque, C.A. *et al.* (2003) Component population study of *Acanthocephalus tumescens* (Acanthocephala) in fishes from Lake Moreno. *Argent. Folia Parasitol.* 50, 72–78
- 20 Settle, W.H. and Wilson, L.T. (1990) Invasion by the variegated leafhopper and biotic interactions – parasitism, competition, and apparent competition. *Ecology* 71, 1461–1470
- 21 Telfer, S. *et al.* (2005) Disruption of a host–parasite system following the introduction of an exotic host species. *Parasitology* 130, 661–668
- 22 Kelly, D.W. *et al.* (2009) Parasite spillback: a neglected concept in invasion ecology? *Ecology* 90, 2047–2056
- 23 Torchin, M.E. *et al.* (2003) Introduced species and their missing parasites. *Nature* 421, 628–630
- 24 Mitchell, C.E. and Power, A.G. (2003) Release of invasive plants from fungal and viral pathogens. *Nature* 421, 625–627
- 25 Blakeslee, A.M.H. *et al.* (2013) Marine invasions and parasite escape: updates and new perspectives. In *Advances in Marine Biology* (66) (Lesser, M., ed.), In pp. 87–169, Academic Press

- 26 Reinhart, K.O. and Callaway, R.M. (2006) Soil biota and invasive plants. *New Phytol.* 170, 445–457
- 27 Maron, J.L. *et al.* (2014) Invasive plants escape from suppressive soil biota at regional scales. *J. Ecol.* 102, 19–27
- 28 Blosssey, B. and Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. *J. Ecol.* 83, 887–889
- 29 Hatcher, M.J. and Dunn, A.M. (2011) *Parasites in Ecological Communities. From Interactions to Ecosystems*, Cambridge University Press
- 30 Werner, E.E. and Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84, 1083–1100
- 31 Hatcher, M.J. *et al.* (2006) How parasites affect interactions between competitors and predators. *Ecol. Lett.* 9, 1253–1271
- 32 MacNeil, C. *et al.* (2003) Parasite-mediated predation between native and invasive amphipods. *Proc. Biol. Sci.* 270, 1309–1314
- 33 MacNeil, C. *et al.* (2003) An acanthocephalan parasite mediates intraguild predation between invasive and native freshwater amphipods (Crustacea). *Freshwater Biol.* 48, 2085–2093
- 34 Abrams, P.A. and Matsuda, H. (1996) Positive indirect effects between prey species that share predators. *Ecology* 77, 610–616
- 35 Hatcher, M.J. *et al.* (2014) Parasites that change predator or prey behaviour can have keystone effects on community composition. *Biol. Lett.* 10, 20130879
- 36 Torchin, M.E. *et al.* (2005) Differential parasitism of native and introduced snails: Replacement of a parasite fauna. *Biol. Invas.* 7, 885–894
- 37 Power, A.G. and Mitchell, C.E. (2004) Pathogen spillover in disease epidemics. *Am. Nat.* 164, S79–S89
- 38 Rudgers, J.A. *et al.* (2005) Mutualistic fungus promotes plant invasion into diverse communities. *Oecologia* 144, 463–471
- 39 Kulmatiski, A. *et al.* (2008) Plant–soil feedbacks: a meta-analytical review. *Ecol. Lett.* 11, 980–992
- 40 Hatcher, M.J. *et al.* (2012) Diverse effects of parasites in ecosystems: linking interdependent processes. *Front. Ecol. Environ.* 10, 186–194
- 41 Kelly, D.W. *et al.* (2006) Invasion by the amphipod *Gammarus pulex* alters community composition of native freshwater macroinvertebrates. *Divers. Distributions* 12, 525–534
- 42 Finkes, L.K. *et al.* (2006) Plant–fungus mutualism affects spider composition in successional fields. *Ecol. Lett.* 9, 344–353
- 43 Rudgers, J.A. *et al.* (2007) Forest succession suppressed by an introduced plant–fungal symbiosis. *Ecology* 88, 18–25
- 44 Janzen, D.H. *et al.* (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528
- 45 Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Population* (den Boer, P.J.G. and Gradwell, G.R., eds), pp. 298–313, Centre for Agricultural Publishing and Documentation Wageningen
- 46 Hudson, P. and Greenman, J. (1998) Competition mediated by parasites: biological and theoretical progress. *Trends Ecol. Evol.* 13, 387–390
- 47 Holt, R.D. and Pickering, J. (1985) Infectious-disease and species coexistence – a model of Lotka–Volterra form. *Am. Nat.* 126, 196–211
- 48 Tompkins, D.M. *et al.* (2000) The role of shared parasites in the exclusion of wildlife hosts: *Heterakis gallinarum* in the ring-necked pheasant and the grey partridge. *J. Anim. Ecol.* 69, 829–840
- 49 Pywell, R.F. *et al.* (2004) Facilitating grassland diversification using the hemiparasitic plant *Rhinanthus minor*. *J. Appl. Ecol.* 41, 880–887
- 50 Mathiasen, R.L. *et al.* (2008) Mistletoes: pathology, systematics, ecology, and management. *Plant Dis.* 92, 988–1006
- 51 Hudson, P.J. *et al.* (2006) Is a healthy ecosystem one that is rich in parasites? *Trends Ecol. Evol.* 21, 381–385
- 52 Dobson, A. *et al.* (2008) Homage to Linnaeus: how many parasites? How many hosts? *Proc. Natl. Acad. Sci. U.S.A.* 105, 11482–11489
- 53 Lafferty, K.D. *et al.* (2006) Parasites dominate food web links. *Proc. Natl. Acad. Sci. U.S.A.* 103, 11211–11216
- 54 Amundsen, P.A. *et al.* (2009) Food web topology and parasites in the pelagic zone of a subarctic lake. *J. Anim. Ecol.* 78, 563–572
- 55 Schmeller, D.S. *et al.* (2014) Microscopic aquatic predators strongly affect infection dynamics of a globally emerged pathogen. *Curr. Biol.* 24, 176–180
- 56 Johnson, P.T.J. *et al.* (2010) When parasites become prey: ecological and epidemiological significance of eating parasites. *Trends Ecol. Evol.* 25, 362–371
- 57 Thielges, D.W. *et al.* (2013) Parasites as prey in aquatic food webs: implications for predator infection and parasite transmission. *Oikos* 122, 1473–1482
- 58 Dunne, J.A. *et al.* (2013) Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biol.* 11, e1001579
- 59 Poulin, R. (2010) Network analysis shining light on parasite ecology and diversity. *Trends Parasitol.* 26, 492–498
- 60 Dobson, A.R. *et al.* (2006) Parasites and food webs. In *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Pascual, M. and Funne, J.A., eds), pp. 119–135, Oxford University Press
- 61 Dunne, J.A. *et al.* (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567
- 62 Keller, R.P. and Perrings, C. (2011) International policy options for reducing the environmental impacts of invasive species. *Bioscience* 61, 1005–1012
- 63 Britton, J.R. (2013) Introduced parasites in food webs: new spades, shifting structures? *Trends Ecol. Evol.* 28, 93–99
- 64 Dobson, A. and Foufopoulos, J. (2001) Emerging infectious pathogens of wildlife. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 356, 1001–1012
- 65 Jones, K.E. *et al.* (2008) Global trends in emerging infectious diseases. *Nature* 451, 990–993
- 66 Childs, J.E. *et al.* (2007) Introduction: conceptualizing and partitioning the emergence process of zoonotic viruses from wildlife to humans. In *Wildlife and Emerging Zoonotic Diseases: The Biology, Circumstances and Consequences of Cross-Species Transmission* (Childs, J.E. *et al.*, eds), pp. 1–31, Springer
- 67 Jeschke, J.M. *et al.* (2013) Novel organisms: comparing invasive species, GMOs, and emerging pathogens. *Ambio* 42, 541–548
- 68 Caffrey, J.M. *et al.* (2014) Tackling invasive alien species in Europe: the top 20 issues. *Manag. Biol. Invas.* 5, 1–20
- 69 Perrings, C. *et al.* (2010) Globalization and Bioinvasions: The International Policy Problem. In *Bioinvasions and Globalization: Ecology, Economics, Management, and Policy* (Perrings, C. *et al.*, eds), pp. 235–250, Oxford University Press
- 70 Gordon, D.R. *et al.* (2008) Consistent accuracy of the Australian weed risk assessment system across varied geographies. *Divers. Distributions* 14, 234–242
- 71 van Lenteren, J.C. *et al.* (2008) Harmonia axyridis: an environmental risk assessment for Northwest Europe. *Biocontrol* 53, 37–54
- 72 Leung, B. *et al.* (2012) TEASing apart alien species risk assessments: a framework for best practices. *Ecol. Lett.* 15, 1475–1493
- 73 Roy, H.E. *et al.* (2012) Invasive alien predator causes rapid declines of native European ladybirds. *Divers. Distributions* 18, 717–725
- 74 Loo, J. (2009) Ecological impacts of non-indigenous invasive fungi as forest pathogens. *Biol. Invas.* 11, 81–96
- 75 Romeis, J. *et al.* (2008) Assessment of risk of insect-resistant transgenic crops to nontarget arthropods. *Nat. Biotechnol.* 26, 203–208
- 76 Essl, F. *et al.* (2011) Review of risk assessment systems of IAS in Europe and introducing the German–Austrian Black List Information System (GABLIS). *J. Nat. Conserv.* 19, 339–350
- 77 Roy, H.E. *et al.* (2014) Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biol.* 20, 3859–3871
- 78 Krebs, J.R. (2011) Risk, uncertainty and regulation. *Philos. Transact. A. Math. Phys. Eng. Sci.* 369, 4842–4852
- 79 Jenkins, E.J. (2015) Wildlife parasites in a one health world. *Trends Parasitol.* 31, 174–180
- 80 Read, A.F. *et al.* (2011) The evolution of drug resistance and the curious orthodoxy of aggressive chemotherapy. *Proc. Natl. Acad. Sci. U.S.A.* 108, 10871–10877
- 81 Hobbs, R.J. *et al.* (2009) Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24, 599–605
- 82 Kueffer, C. and Kaiser-Bunbury, C.N. (2014) Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. *Front. Ecol. Environ.* 12, 131–137
- 83 Tsangaras, K. *et al.* (2014) Negative purifying selection drives prion and doppel protein evolution. *J. Mol. Evol.* 79, 12–20
- 84 Hilderbrand, R.H. *et al.* (2005) The myths of restoration ecology. *Ecol. Soc.* 10, 19
- 85 Hughes, F.M.R. *et al.* (2012) When is open-endedness desirable in restoration projects? *Restoration Ecol.* 20, 291–295
- 86 Keesing, F. *et al.* (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468, 647–652

- 87 Randolph, S.E. and Dobson, A.D.M. (2012) Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology* 139, 847–863
- 88 Ostfeld, R.S. and Keesing, F. (2012) Effects of host diversity on infectious disease. *Annu. Rev. Ecol. Evol. Syst.* 43, 157–182
- 89 Lafferty, K.D. and Wood, C.L. (2013) It's a myth that protection against disease is a strong and general service of biodiversity conservation: response to Ostfeld and Keesing. *Trends Ecol. Evol.* 28, 503–504
- 90 Wood, C.L. and Lafferty, K.D. (2013) Biodiversity and disease: a synthesis of ecological perspectives on Lyme disease transmission. *Trends Ecol. Evol.* 28, 239–247
- 91 Ostfeld, R.S. and Keesing, F. (2013) Straw men don't get Lyme disease: response to Wood and Lafferty. *Trends Ecol. Evol.* 28, 502–503
- 92 Dobson, A. (2004) Population dynamics of pathogens with multiple host species. *Am. Nat.* 164, S64–S78
- 93 Holt, R.D. *et al.* (2003) Parasite establishment in host communities. *Ecol. Lett.* 6, 837–842
- 94 Mitchell, C.E. *et al.* (2002) Effects of grassland plant species diversity, abundance, and composition on foliar fungal disease. *Ecology* 83, 1713–1726
- 95 Suzan, G. *et al.* (2009) Experimental evidence for reduced rodent diversity causing increased hantavirus prevalence. *PLoS ONE* 4, e5461
- 96 Johnson, P.T.J. and Hoverman, J.T. (2012) Parasite diversity and coinfection determine pathogen infection success and host fitness. *Proc. Natl. Acad. Sci. U.S.A.* 109, 9006–9011
- 97 Wolfe, N.D. *et al.* (2007) Origins of major human infectious diseases. *Nature* 447, 279–283
- 98 Simpson, J.A. and Weiner, E.S. (1989) In *The Oxford English Dictionary* (2), Clarendon Press
- 99 Gray, D.K. *et al.* (2007) Efficacy of open-ocean ballast water exchange as a means of preventing invertebrate invasions between freshwater ports. *Limnol. Oceanogr.* 52, 2386–2397
- 100 Bailey, S.A. *et al.* (2011) Evaluating efficacy of an environmental policy to prevent biological invasions. *Environ. Sci. Technol.* 45, 2554–2561
- 101 Okamura, B. and Feist, S.W. (2011) Emerging diseases in freshwater systems. *Freshwater Biol.* 56, 627–637
- 102 Branson, J. and Clough, P. (2006) *Didymosphenia geminata Economic Impact Assessment. Final Report for Biosecurity New Zealand*, Inst. Econ. Res.
- 103 Anderson, L.G. *et al.* (2014) Biosecurity and vector behaviour: evaluating the potential threat posed by anglers and canoeists as pathways for the spread of invasive non-native species and pathogens. *PLoS ONE* 9, e92788
- 104 Anderson, L.G. *et al.* (2014) *Evaluating the Effectiveness of Hot Water as a Decontamination Method to Prevent the Accidental Movement of Aquatic Invasive Species*, Report to the UK Department of Environment Food and Rural Affairs from The University of Leeds and the Centre for Environment Fisheries and Aquaculture Science
- 105 Slovic, P. (1987) Perception of risk. *Science* 236, 280–285
- 106 McDaniels, T. *et al.* (1995) Characterizing perception of ecological risk. *Risk Anal.* 15, 575–588
- 107 Gozlan, R.E. *et al.* (2013) Understanding the threats posed by non-native species: public vs. conservation managers. *PLoS ONE* 8, e53200
- 108 Tversky, A. and Kahneman, D. (1981) The framing of decisions and the psychology of choice. *Science* 211, 453–458