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INVASIONS AND INFECTIONS

Invading with biological weapons: the importance of disease-mediated invasions

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Summary

1. Invasive organisms and emerging wildlife disease pose two of the greatest threats to global biodiversity and ecosystem functioning.
2. Typically, when parasites are considered in invasion biology, it is in the context of the enemy release hypothesis, wherein a non-indigenous species has greater probability of invasion success by virtue of leaving its natural enemies, including parasites, behind.
3. It is also possible that native parasites may prevent invasions, but it is clear that invasive organisms may bring infectious diseases with them that can infect native competitors (via spillover), or act as competent hosts for native diseases, increasing disease prevalence among native species (via spillback).
4. If the shared disease (either via spillover or spillback) has higher virulence in the native host (which is particularly likely with introduced parasites), there is the potential that the disease can act as a 'biological weapon' leading to a disease-mediated invasion (DMI).
5. Here, we review cases where disease may have been an important factor mediating a wide range of invasions in vertebrates, invertebrates and plants.
6. We then focus on the invasion of the grey squirrel into the UK as a case study of a DMI, and we discuss how mathematical models have helped us to understand the importance of this shared disease and its implications for the management of invasive species.
7. We conclude that (i) DMIs are a widespread phenomenon, that (ii) spillover is more common in animal invasions and spillback more common among plant invasions and that (iii) spillover DMIs are particularly important in explaining the replacement of native animals with phylogenetically similar non-indigenous species.

Key-words: competition, conservation, disease-mediated invasions, enemy alliance, extinctions, invasive species, modelling parasites, replacement, spillback, spillover

Introduction

The importance of infectious disease in shaping human history and determining the movements and invasions of human populations is clear. The tsetse fly belt discouraged the Bantu from invading Southern Africa (Diamond 1999), and Malaria in the British forces aided Washington's victory at Yorktown (McNeill 2010). During the age of exploration, European conquistadors invaded the Americas and introduced diseases such as smallpox that decimated Native American populations (Diamond 1999; Riley 2010). Resistance to these diseases was not the only advantage that the Europeans had over Native Americans, but it certainly contributed to the speed and ubiquity of the conquest. The invading Europeans inadvertently brought biological weapons – their diseases – with them, and concurrently, the emergence of disease within the native populations mediated the Europeans' invasion.

Parallel scenarios also unfold in natural communities. Although the concept of parasite-mediated competition has been reviewed in the past (Freeland 1983; Price *et al.* 1986, 1988), it is now becoming apparent that disease, specifically diseases as biological weapons, may also be a common factor mediating species invasions (Prenter *et al.*

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2004; Hatcher, Dick & Dunn 2006; Dunn 2009). Here, we firstly review the role of disease-mediated invasions (hereafter DMIs) in natural communities. Next, we discuss how mathematical models have been applied to the best studied example of a DMI: the invasion of grey squirrels into the UK, and argue that the models were critical in highlighting the importance of the disease. Our twin aims are to highlight the importance of DMIs and to make a case for the use of modelling to benefit conservation efforts in the face of disease.

The role of parasites in invasions

Recently there has been an increasing interest in the roles that disease can play in both animal (Prenter *et al.* 2004; Hatcher, Dick & Dunn 2006; Dunn 2009) and plant (Eppinga *et al.* 2006) invasions. For the duration of the review, we will refer to all infectious organisms (parasites, pathogens, parasitoids, etc.) as 'parasites' for simplicity, except when we refer to specific examples, although we acknowledge the distinctions suggested by others (Lafferty & Kuris 2002). Likewise, we refer to non-native plants and animals generally as 'non-indigenous species', and only use the phrase 'invasive species' when referring to specific species that have indeed become invasive (Kolar & Lodge 2001). By far the most studied way in which parasites influence invasions is through their absence (Wolfe 2002; Mitchell & Power 2003; Torchin *et al.* 2003; Torchin & Mitchell 2004). Parasites along with predators and herbivores are the key component of the 'enemy release hypothesis', where the non-indigenous species gains an advantage because it arrives in a new habitat without its natural enemies. There have been a number of excellent reviews (Wolfe 2002; Mitchell & Power 2003; Torchin *et al.* 2003; Torchin & Mitchell 2004) that discuss how leaving behind parasites can have an important impact on invasions.

But how else may natural enemies and in particular disease be involved in invasion? Clearly, when a non-indigenous species enters a new environment, it will encounter herbivores or predators and also parasites that it has not previously encountered. We might expect that some of these parasites (especially generalist parasites) will be able to infect the non-indigenous species, that the non-indigenous host will have little resistance against these novel parasites and that infection and disease could thus prevent the non-indigenous species from becoming invasive. For instance, it has long been recognized that native diseases can prevent introduced farm animals from flourishing in their non-native ranges (cattle in Africa limited by trypanosomiasis (Ford 1971); domestic ducks in Michigan limited by a *Leucocytozoon* protozoon (Chernin 1952)). There are, however, fundamental problems in assessing how important this process is in nature; it is very difficult to study failures to invade. An analysis of the data on the potential role of parasites in failed introductions would be an interesting contribution to the invasion biology literature.

If the generalist parasite does not prevent the non-indigenous species from establishing in its new range, then the non-indigenous host has the potential to interact with the native host, indirectly via their shared parasite(s). If the non-indigenous host is a poor reservoir for the parasite, then its presence could decrease infection prevalence in the native host population via a dilution effect (Ostfeld & Keesing 2000; Keesing *et al.* 2006). For instance, ladybirds introduced to North America (*Harmonia axyridis*) serve as a sink for eggs of a parasitoid (*Dinocampus coccinellae*) shared with the native ladybird (*Coleomegilla maculate*) (Hoogendoorn & Heimpel 2002), and roundhead galaxias fish in New Zealand (*Galaxias anomalus*) are parasitized by fewer helminths when they co-occur with introduced brown trout (*Salmo trutta*) (Kelly *et al.* 2009a). In these examples, disease does not facilitate invasion of the non-indigenous host, because dilution benefits the native host.

However, it is also possible that the non-indigenous species could become infected with a native parasite and transmit disease back to the native fauna or flora (Kelly *et al.* 2009b). If such a disease were less virulent in the non-indigenous species (or the non-indigenous host were a more competent reservoir), such a 'spillback' of the parasite may in principle facilitate the invasion (see Eppinga *et al.* 2006 and the 'accumulation of native pathogens hypothesis'). This is especially true if the non-indigenous species can gain advantage over its native competitors via apparent competition (Holt 1977) mediated by their shared parasites. We define this phenomenon as a 'spillback DMI'.

The other way in which disease can facilitate an invasion occurs when the infectious parasite is introduced along with its non-indigenous host. Disease can then 'spillover' from the non-indigenous host species (Power & Mitchell 2004) to infect susceptible native competitors, increasing the probability of a successful invasion (again, via apparent competition). When a non-indigenous parasite is able to infect both non-indigenous and native hosts, we might expect it to be more virulent among the natives. This is because most invasions occur when small populations survive difficult journeys or escape from introduced populations; non-indigenous species infected with virulent parasites are likely to die during the translocation process, and managed populations are unlikely to be maintained with virulent parasites. Therefore, only relatively avirulent parasites are likely to accompany hosts to new ranges. Although these avirulent parasites are likely to be understudied or unknown, due to their minimal effects on their original hosts, they may have the potential to cause virulent infectious diseases in native species, due to native species' lack of previous exposure or innate physiological differences. Then, the non-indigenous parasites can become a biological weapon and lead to a scenario we describe as a 'spillover DMI.'

Spillover DMIs are of particular concern for conservation biology, because the parasites causing emergent diseases are non-indigenous species themselves. Because

parasites are generally much smaller than other non-indigenous species, they are arbitrarily classified as emergent diseases instead of invasive species. However, the only fundamental difference between invasive species and emergent diseases is that an emergent disease (parasite) requires competent hosts to spread, while an invasive species requires some other mechanism to facilitate its invasion. Spillover DMIs are clear examples of invasional meltdown (Simberloff & Von Holle 1999; Simberloff 2006), in which the indirect effect of one species (the parasite) facilitates the invasion of a second species (the non-indigenous host) and the invasion of the host likewise facilitates the invasion/emergence of the parasite/disease.

We consider both spillback and spillover DMIs to be cases of 'invading with biological weapons'. In both categories, rather than the non-indigenous species benefiting from 'enemy release', the invader benefits from an 'enemy alliance': an indirect mutualism than can simultaneously lead to a species invasion and the outbreak of disease.

Examples of DMIs

Our goal in this section is to provide a comprehensive review of known spillover and spillback DMIs, in which a non-indigenous species has gained an advantage over a native competitor by virtue of using a shared parasite as a biological weapon. We do not include 'indirect DMIs' that involve additional species; for instance, if a parasite were able to infect both native and non-indigenous hosts, but only able to modify the behaviour/physiology of its native host, it could render the native host more susceptible to predation by a fourth species and indirectly mediate invasion success of the non-indigenous host (Rigaud & Moret 2003; Mouritsen & Poulin 2005). Although fascinating, the complexity of this type of interaction is beyond the scope of this review. We also refrain from reviewing invasions in which the parasite is host-specific and only capable of infecting the native species.

Although spillback and spillover DMIs have received relatively little attention in the invasion biology literature, they have occurred repeatedly throughout ecological history and continue to threaten biodiversity and ecosystem health today. Examples of DMIs can be found broadly across taxa; the disease-causing organisms may be microparasites, macroparasites, parasitoids or even soil pathogens, and host species may be vertebrate animals (reviewed in Table 1), invertebrates (reviewed in Table 2) or plants (reviewed in Table 3). These tables are presented chronologically, beginning with historical DMIs, focusing on current and ongoing DMIs and concluding with more speculative DMIs.

The earliest recorded DMI was the late 18th century invasion of introduced European birds on the Hawaii islands, mediated by avian malaria and birdpox epidemics in the native Hawaiian finches (Drepanidinae) (Warner 1968). Now, the remaining Drepanidinae are restricted to high elevation sites, beyond the range of the disease vectors, while native species dominate the lowlands (van Riper *et al.* 1986). Other historical DMIs include the invasion of the introduced starry sturgeon (*Acipenser stellatus*) into the Aral Sea in 1934, mediated by die-offs of the native bastard sturgeon (*Acipenser nudiventris*) caused by the shared monogenean, *Nitzschia sturionis* (Bauer, Pugachev & Voronin 2002; Pourkazemi 2006), and also the dramatic range of expansion of North American white-tailed deer (*Odocoileus virginianus*) in the mid-1900s and its near total replacement of moose (*Alces alces*) and caribou (*Rangifer turandis*) in the north-eastern United States due to transmission of a shared meningeal worm, *Parelaphostrongylus tenuis* (Anderson 1972).

Some of these historical DMIs are now threatening to become problematic again. For example, *P. tenuis*, the meningeal worm of cervids, has now been identified in mule deer (*Odocoileus hemionus*) in sympatry with white-tailed deer in Nebraska, as white-tailed deer continue to expand westward (Oates, Sterner & Boyd 2000). Likewise, crayfish plague, caused by a fungus (*Aphanomyces astaci*), decimated European crayfish populations when North American crayfish were introduced to Italy in the 1860s; now, invasive signal crayfish (*Pacifastacus leniusculus*) and red swamp crayfish (*Procambarus clarkia*), which are reservoirs for *A. astaci*, threaten to replace susceptible native crayfish species in the UK (Holdich & Reeve 1991), Eastern Europe (Parvulescu *et al.* 2012) and Northern Europe (Vralstad *et al.* 2011). Finally, although common pheasants (*Phasianus colchicus*) were introduced to the UK at least one thousand years ago, it has only recently been determined that their competitive superiority over native grey partridges (*Perdix perdix*) is in part due to pheasants being a reservoir for a shared nematode (*Heterakis gallinarum*) that has been linked to partridge declines (Tompkins, Draycott & Hudson 2000; Tompkins, Greenman & Hudson 2001).

Some current, ongoing DMIs are among the most well-known and best recorded examples of DMIs. Grey squirrels (*Scurius carolinensus*) from North America threaten to replace native red squirrels (*Scurius vulgaris*) in the UK, in part due to the transmission of a *Parapoxvirus* that is lethal to reds but not to greys (Tompkins *et al.* 2002; Tompkins, White & Boots 2003). This system is discussed as a case study in the final section of this review. Variegated leafhoppers (*Erythroneura variabilis*) from Mexico have invaded vineyards in Southern California and are replacing the native grape leafhoppers (*Erythroneura elangantula*) due to a combination of resource competition and apparent competition mediated by a shared egg parasitoid (*Anagros epos*) (Settle & Wilson 1990). California grasslands are being invaded by Eurasian grasses (including *Avena fatua* and members of the genus *Bromus*), which harbour dense aphid populations; these aphids are vectors of barely/cereal yellow dwarf viruses (B/CDYVs) that then spillback and infect the native grasses, which are more susceptible than the invasive grasses due to differences in seasonality (Malmstrom *et al.* 2005a,b). Finally,

Table 1. Disease-mediated invasions of vertebrate hosts

Native host and host range	Non-indigenous host, origen and date of introduction (if historical)	Parasite/disease	Consequences/complications	Spillover/ spillback Host similarity Reference(s)
Endemic Hawaiian finches (over 50 species of Drepanidinae)	Domestic birds introduced from Europe in late 18th century, incl. house finch (*Carpodacus mexicanus)*, Japanese white-eye (*Zosterops japonicas*) etc.	Avian malaria (*Plasmodium relictum);* Birdpox (*Haemoproteus spp).* *Both diseases are vector-borne	Over half of endemic Hawaiian bird species have gone extinct, in large part due to exposure to avian malaria and pox. Native species are more abundant at higher altitude sites (beyond range of the vectors and disease); non-indigenous species are more resistant to disease and more abundant at lower altitude sites Habitat loss and other factors may have been more critical for the initial loss of species, but disease continues to limit bird distributions today. Diseases are vector-borne: introduced mosquitoes (*Culex pipiens fatigans*) vector malaria and flies (Hippoboscidae) vector birdpox.	Spillover Family (Fringlidae) Warner (1968) and van Riper *et al.* (1986)
Bastard sturgeon *Acipenser nudiventris* in the Aral Sea	Starry sturgeon *Acipenser stellatus* introduced from the Caspian Sea in 1934	Monogenean gill fluke (*Nitzschia sturionis*)	Starry sturgeon were introduced to the Aral Sea in 1934 and brought the gill fluke with them; native bastard sturgeon had no prior exposure and were decimated by disease. More recently, all sturgeon populations in the Caspian Sea region have declined dramatically, due to pollution, dam construction and overharvesting. Original records were written in Russian and are not translated into English.	Spillover Genus (*Acipenser*) Bauer, Pugachev & Voronin (2002) and Pourkazemi (2006)
Moose (*Alces alces*) and Caribou (*Rangifer turandis*) in north-eastern North America	White-tailed deer (*Odocoileus virginianus*) expanding beyond their historical range in mid-1900s	Meningeal worm *Parelapho-strongylus tenuis*	White-tailed deer are hosts for the meningeal worm and do not get sick, but transmit it to moose and caribou, which are very susceptible to disease. Deer became the dominant cervids in areas where other species used to be more abundant; moose and caribou declined. Deer range expansion is also attributed to land use change. Great plains seemed like a barrier for spread of the worm, but recently, disease has also been found in mule deer (*O. hemionus*) in Nebraska.	Spillover Family (Cervidae) Anderson (1972) and Oates, Sterner & Boyd (2000)

(continued)

Table 1 (continued)

Native host and host range	Non-indigenous host, origen and date of introduction (if historical)	Parasite/disease	Consequences/complications	Spillover/ spillback Host similarity Reference(s)
Grey partridges (*Perdix perdix)* in UK	Common pheasants (*Phasianus colchicus*) historically introduced from Asia	Caecal nematode (*Heterakis gallinarum*)	Pheasants are reservoirs for a shared nematode, but partridges are more susceptible to disease; partridges have declined for at least 50 years. Pheasants became established prior to the known emergence of the disease, but could still benefit from apparent competition. Hosts may also share additional parasites. Decline in partridges is also attributed to habitat change (agriculture), increased predation risk, nest parasitism and resource competition with pheasants.	Spillover Family (Phasianinae) Kimmel (1988), Tompkins, Draycott & Hudson (2000) and Tompkins, Greenman & Hudson (2001)
Red squirrels (*Sciurus vulgaris*) in UK	Grey squirrels (*Scurius carolinensus*) from North America	Squirrelpox (*parapoxvirus*)	Grey squirrels are replacing red squirrels across much of their range in the UK. The virus is virulent for native red squirrels, but grey squirrels are a reservoir. Grey squirrels are the superior resource competitor, but their resistance to the disease may be increasing the rate of invasion. The virus was likely introduced along with grey squirrels from North America.	Spillover Genus (*Scurius*) Tompkins *et al.* (2002) and Tompkins, White & Boots (2003)
Sunbleak (*Leucaspius delineates*) throughout Europe	Topmouth gudgeon (*Pseudorasbora parva*) introduced from Asia	Intracellular eukaryotic pathogen (*Sphaerothecum destruens)*	Gudgeon were introduced for commercial aquaculture and carry the pathogen. Exposure to holding water conditioned by gudgeon (and its parasites) is sufficient to infect sunbleak; infection in sunbleak inhibits spawning and causes death. Gudgeon are now invasive throughout Europe; invasions are associated with local extinctions of sunbleak.	Spillover Family (Cyprinidae) Gozlan *et al.* (2005)
Speculative: Amphibian diversity around the world; e.g. yellow belly frog (*Elachistocleis bicolor*) in Argentina	American bullfrogs (*Rana catesbeiana*, renamed *Lithobates catesbeiana*), from North America	Amphibian chytrid fungus, Bd (*Batrachochytrium dendrobatidis*) causing chytridiomycosis Bullfrogs may also spread *Ranavirus*	*Bd* threatens global amphibian diversity, but some species are more susceptible to chytridiomycosis than others. Bullfrogs carry *Bd* and *Ranavirus* and have been introduced around the world. Transmitting *Bd* to local amphibians may explain emergence of the disease and recent invasions (like in Argentina). Bullfrogs may not compete directly with all species that could contract chytridiomycosis (e.g. tree frogs, family Hylidae); however, *Bd* could facilitate replacement of other indigenous true frogs (family Ranidae) with bullfrogs.	Spillover Class (Amphibia) or Faimily (Ranidae) Arellano *et al.* (2009), Schloegel *et al.* (2009) and Akmentins & Cardozo (2010)

*Diseases transmitted by vectors

Table 2. Disease-mediated invasions of invertebrate hosts

Native host and host range	Non-indigenous host, origen and date of introduction (if historical)	Parasite/disease	Consequences/ complications	Spillover/spillback Host similarity Reference(s)
Atlantic stream crayfish (*Austropotamobius pallipes*), European crayfish (*Astacus astacus*), and other European crayfish species	Signal crayfish (*Pacifastacus leniusculus*), red swamp crayfish (*Procambarus clarkii*) and other North American crayfish species	Crayfish plague fungus (*Aphanomyces astaci*)	Initial outbreaks of plague destroyed Central European crayfish populations in the 1860s when American crayfish were imported into Italy. Invasive crayfish from North America are resistant to disease and threaten to replace native species. Crayfish plague has recently emerged in Eastern Europe and in the UK. Invasions can also be attributed to fast growth rate and superior competitive ability of the non-indigenous species.	Spillover Family (Astacidae) or Genus (*Astacus*) Holdich & Reeve (1991), Gherardi (2006), Vralstad *et al.* (2011) and Parvulescu *et al.* (2012)
Grape leafhoppers, GLH *Erythroneura elangantula)*, in the San Joaquin Valley, California	Variegated leafhoppers, VLH (*Erythroneura variabilis)* from northern Mexico	Egg parasitoid (*Anagrus epos)*	The parasitoid usually prevents GLH from damaging crops. Invasive VLH is less susceptible to the parasitoid, but more damaging to crops. In the absence of the parasitoid, VLH and GLH are equal competitors, but with the parasitoid present, VLH replaces GLH due to the addition of apparent competition.	Spillback Genus (*Erythroneura*) Settle & Wilson (1990)
Speculative: Native honeybees (*Bombus spp.*) incl. *B. rufocinctus*, *B. bimaculatus,* and *B. fervidus* in western North America	Commercially raised honeybees (*Bombus impatiens*) native to eastern North America; also introduced to Central and South America	Trypanosome, *Crithidia bombi* and microsporidian *Nosema bombi*	Commercial *B. impatiens* escape from greenhouses in their native and non-native ranges, but it is not clear whether these populations persist. *C. bombi* is found in the majority of commercial bees that do not exhibit symptoms, but many wild bees are more susceptible. Parasitism in wild bees is highest near greenhouses, indicative of spillover. Many other factors also contribute to bee declines (habitat loss, other parasites, colony collapse disorder, etc.)	Spillover/Spillback (depends on range) Genus (*Bombus*) Otterstatter & Thomson (2008) and Meeus *et al.* (2011)

Table 3. Disease-mediated invasions of plant hosts

Native host and host range	Non-indigenous host, origen, and date of introduction (if historical)	Parasite/disease	Consequences/complications	Spillover/spillback Host similarity Reference(s)
California native bunchgrasses, incl. *Elymus glaucus, Elymus multisetus* and *Nassella pulchra*	Invasive grasses from Eurasia incl. *Avena fatua* and *Bromus sp.*	Barley/cereal yellow dwarf viruses (B/CYDVs) *Vectored by native aphids	California grasslands are being invaded by non-native grasses. Aphid populations are much higher in invasive grasses, which doubles disease incidence among native grasses. Invasion is also attributed to disturbance and the outcome of resource competition, but B/CYDVs may increase the rate of invasion. B/CYDVs were likely present in California prior to the invasion. Both natives and invasives are stunted by viral infection; direct cost of aphid densities is unclear.	Spillback Family (Poaceae) Malmstrom *et al.* (2005a,b, 2007)
Native plants in Western Ghats of India, incl. *Amaranthus sp.* and *Bambusa sp.*	Siam Weed (*Chromolaena odorata*) from North America	Native fungal soil pathogens (genus F*usarium,* tentatively *F. semitectum)*	Pathogen density is much higher near *C. odorata,* which inhibits growth of surrounding native plants and reduces diversity. The invasive plant may stimulate the pathogen through root exudates. Life history (vegetative propagation rather than seedlings) may protect the invasive plant from fungus.	Spillback Division (Angiospermae) Mangla, Inderjit & Callaway (2008)
Coastal dune plants in Mediterranean Europe, incl. *Cistus salviifolius* and *Ammophila arenaria*)	Ice plant (*Carpobrotus edulis*) from South Africa	Native soil biota, incl. putatively pathogenic root chytrid fungi (Order Chytridiales)	Invasive ice plant initially grows better on sterilized soil, but then forms positive feedback with soil biota. Ice plants that have been established longer in their invasive ranges have more root chytrids. Native plants grown in soil conditioned by ice plants have lower fitness. Soil feedback could also be due to allelopathy or inhibition of beneficial mycorrhizae, but pathogenic chytrids likely play a role, especially for decrease in fitness in *C. salviifolius.*	Spillback Division (Angiospermae) de la Pena *et al.* (2010)
Native plants in Yunnan, China, incl. *Lolium perenne*, *Eupatorium fortune* and *Medicago sativa*	Eupatory (*Ageratina adenophora*) from Mexico	Native soil biota incl. vesicular arbuscular mycorrhizal fungi (VAM) and bacteria	Native soil biota inhibit growth of native plants but not the eupatory. Positive feedback loop allows eupatory to dominate understory. Invaded soils have higher VAM abundance and higher fungi/bacteria ratio; invaded soils also have altered nutrient content, but sterilization experiment confirms that change in soil microbial community is most inhibiting. Specific pathogens are unidentified.	Spillback Division (Angiospermae) Niu *et al.* (2007)
Speculative: Blue bunchgrass (*Festuca idahoensis*) and other grasses in north-western American prairies	Spotted knapweed (*Centaurea maculosa*) from Eastern Europe	Native soil biota, incl. arbuscular mycorrhizal fungi (AMF)	The invasive plant has enhanced competitive ability when associating with native soil fungi, reducing native plant cover and diversity. Soil fungi do not affect growth of native or invasive species when grown alone, but when grown together, soil fungi enhance competitive ability of the invasive; this emergent property is not fully understood. Invasion is also attributed to allelopathy and resource competition Specific pathogens are unidentified.	Spillback Division (Angiospermae) Marler, Zabinski & Callaway (1999) and Callaway *et al.* (2004)

*Diseases transmitted by vectors

the sunbleak (*Leucaspius delineates*) was once a common fish in European freshwater systems; now however, it is threatened by the Asian topmouth gudgeon (*Pseudorasbora parva*) and the generalist intracellular pathogen it carries (*Sphaerothecum detruens*). Local invasions by *P. parva* are often accompanied by local extinctions of *L. delineates* because the shared pathogen is much more virulent towards *L. delineates* (Gozlan *et al.* 2005).

New molecular techniques and increasing ecological interest in plant–soil interactions have led to the discovery of several plant DMIs in which non-indigenous plants appear to use native soil pathogens as biological weapons against native species (Eppinga *et al.* 2006). North American Siam weed (*Chromolaena odorata*) is invasive in the Western Ghats of India, where it increases the abundance of a fungal soil pathogen (tentatively identified as *Fusarium semitectum*) that inhibits growth of native plants (Mangla, Inderjit & Callaway 2008). Ice plant (*Carpobrotus edulis*) from South Africa is invasive in Mediterranean Europe where it forms a positive feedback loop with the local soil biota, inhibiting growth of native species including *Cistus salviifolius*. Soils conditioned by *C. edulis* have a higher density of putatively pathogenic root fungi of order Chytridiales (de la Pena *et al.* 2010). Mexican eupatory (*Ageratina adenophora*) is invasive in Yunnan, China, where a similar positive feedback loop with the local soil biota results in more dense vesicular arbuscular mycorrhizal fungi and a higher soil fungi : bacteria ratio. Sterilization experiments show that this change in soil biota directly inhibits local plant species (Niu *et al.* 2007). In north-western American prairies, invasive spotted knapweed (*Centaurea maculosa*) from Eastern Europe forms a complex with the native soil biota, in particular arbuscular mycorrhizal fungi, which increase the invader's competitive ability relative to the native bunchgrass, *Festuca idahoensis* (Marler, Zabinski & Callaway 1999). We classify this last example is a speculative DMI, because the effect of specific soil pathogens has not yet been confirmed; this may even be an example of an indirect DMI, if the dynamics of the below-ground community are sufficiently complex.

We have included two other speculative DMIs in our review, one with implications for the global decline in amphibian diversity and one with implications for the decline in plant–pollinator diversity. Chytridiomycosis, an amphibian disease caused by the fungus *Batrachochytrium dendrobatidis* (*Bd*), has recently emerged and already poses one of the greatest threats ever to global amphibian diversity. American bullfrogs (*Lithobates catesbeiana*), which are a reservoir for *Bd* (Garner *et al.* 2006), are native to the Eastern United States but invasive in many other parts of the world, including South America (Akmentins & Cardozo 2010). Recently, a range of *Bd* strains have been identified in non-indigenous populations of bullfrogs in South America (Schloegel *et al.* 2010; Ghirardi *et al.* 2011) and Asia (Goka *et al.* 2009; Bai *et al.* 2012). In Argentina, bullfrogs have recently invaded (Akmentins & Cardozo 2010), bullfrogs carry *Bd* (Ghirardi *et al.* 2011), and *Bd* appears to cause mortality in at least one species of local amphibian, the yellow belly frog (*Elachistocleis bicolor*) (Arellano *et al.* 2009), although bullfrogs have not been directly implicated. Commercially raised bumblebees are descendents of *Bombus impatiens* from eastern North America. This species is used widely in greenhouses throughout the Americas, and escapes from greenhouses permit *B. impatiens* to interact with native bee species, including *B. rufocinctus*, *B. bimaculatus* and *B. fervidus* in the Western United States. *Crithidia bombi* and *Nosema bombi* (a trypanosome and a microsporidian) have been implicated in bee declines and both occur at high prevalence within commercial colonies. Furthermore, both parasites can spillover to infect native bee species when *B. impatiens* escape greenhouses (Otterstatter & Thomson 2008; Meeus *et al.* 2011). However, it is not clear whether these escaping bees have successfully established colonies, so again this remains as a speculative DMI.

In reviewing DMIs (Tables 1–3), several patterns emerge (speculative DMIs are excluded from these analyses). For instance, most disease-mediated animal invasions (seven of eight animal DMIs), including invasive grey squirrels in the UK (Tompkins, White & Boots 2003) and invasive New World crayfish species in Europe (Holdich & Reeve 1991), benefit from spillover, rather than spillback. In contrast, most disease-mediated plant invasions (all four plant DMIs), including invasive *C. odorata* in India (Mangla, Inderjit & Callaway 2008) and invasive *A fatua* in California (Malmstrom *et al.* 2007), benefit from spillback. Spillover-mediated invasions may be less likely among plants than animals because non-indigenous plants can be introduced to their non-native range as seeds and may not be accompanied by the same avirulent parasites, especially soil pathogens, that infect them in their native ranges. In contrast, non-indigenous animal species are often introduced as adults (e.g. domestic birds introduced to Hawaii (Warner 1968)) or escape from managed commercial populations (e.g. crayfish imported into Europe (Holdich & Reeve 1991)) and are more likely to already carry parasites from their home ranges with them.

It is also apparent that the DMI concept seems particularly useful in explaining animal invasions in which the non-indigenous species is phylogenetically similar to the native species it is replacing (e.g. grey squirrels replacing red squirrels in the UK (Tompkins, White & Boots 2003); variegated leafhoppers replacing grape leafhoppers in Southern California (Settle & Wilson 1990)). This is consistent with the observation that physiologically similar species compete for the same resources and can also be infected with the same parasites (Freeland 1983). In the case of DMIs, disease may be able to tip the competitive balance in favour of the more resistant host species, such that ecological replacement is catalysed by parasite-mediated apparent competition. However, replacement by a phylogenetically similar exotic species appears less common among plant invasions. Four of the eight animal DMIs describe the replacement of a native species with a

non-indigenous congeneric; the other four non-indigenous animals are in the same family as the native species they are replacing. In contrast, none of the four plant DMIs describe the replacement of native species with a non-indigenous congeneric; moreover, three of the non-indigenous plants are only related to the native species they are replacing at the division level. Because invasive plants seem to benefit from being phylogenetically unique from native species assemblages (Strauss, Webb & Salamin 2006), perhaps diseases are more likely to mediate invasions of plants that have already become established by virtue of their phylogenetic uniqueness. This pattern of host similarity could also be related to differences in animal and plant immune systems and parasite specificity.

Invading with a biological weapon–case study squirrels

Probably the best studied example of disease-mediated native replacements is the invasion of grey squirrels into the UK and subsequent decline and regional extinction of red squirrels. Because of its introduction into the UK, the grey squirrel has 'replaced' the red squirrel throughout most of England and Wales and in parts of Scotland and Ireland (Bryce 1997; O'Teangana *et al*. 2000; Gurnell *et al*. 2004). There are now only restricted areas in which the red squirrel survives, and maintaining these populations is a conservation priority (DEFRA 2007; Parrott *et al*. 2009). Greys are present in England and as far north as Central and Eastern Scotland (Lurz 2010). Reds remain in isolated patches in South and Central Scotland and in large continuous populations in Northern Scotland (Lurz 2010). The UK red/grey/squirrelpox system represents the classic situation in which a DMI may be occurring. There is a native (red) and invading (grey) species that compete for resources, and the squirrelpox virus which was introduced along with the invader causes high mortality in the native species. Squirrelpox virus is present in greys in England and spreading into southern Scotland with sporadic outbreaks of squirrelpox in the red populations in these regions (McInnes *et al*. 2009).

The disease was not traditionally part of the explanation for the red decline probably because it is rarely seen in the wild. Infected red squirrels suffer from obvious scabs and lesions around the face, feet and genitals, but the disease has a low prevalence (Sainsbury & Gurnell 1995). Faced with a rare disease, it is perhaps natural to feel that it has not played an important role in the dramatic decline we have observed. However, classic ecological theory predicts that highly virulent diseases will have a low visibility, because they kill individuals quickly, but are more likely to be involved in regulating host populations (Anderson & May 1981). Such general theoretical models are designed to examine what the impacts of different biological processes are likely to be in general. But they are also well suited to examining our key question of whether the disease is likely to have been important in the replacement of the red squirrel despite its low prevalence. Using this approach, Tompkins, White & Boots 2003; argued that squirrel pox is implicated in the rapid replacement of red populations. The number of infections was predicted to be low in the model (Tompkins, White & Boots 2003), yet the effect on the population dynamics was marked, emphasizing within this system-specific model that low visibility does not imply low importance of the disease. It is likely that the difficulty in observing such infections in the field often results in disease being overlooked. In the case of squirrel pox, it took over 50 years for the first observation of disease (Middleton 1930) to the identification of the virus (Scott, Keymer & Labram 1981), a further 14 years before its impact on red population persistence was suggested (Sainsbury & Gurnell 1995) with the current view that squirrel pox is unequivocally linked to the replacement of red squirrels (Bosch & Lurz 2012).

Understanding the role of the shared disease in the replacement of red by grey squirrels in the UK is a good example of how models can play an important role in understanding problems in population ecology. For a complete understanding of an ecological problem a combination of observation, experimentation and theoretical modelling would be optimal. In conservation problems such as the red squirrel replacement, there is often observational data, but there is no opportunity of designing and carrying out experiments. There is the potential for natural experiments if disease is not present in all populations because we can gain some insight to be gained from comparison of these populations. Without a natural experiment where the disease becomes introduced to the disease-free population (see Settle & Wilson 1990), however, the only two routes we can take are to improve the observation of the system with more systematic surveys and to use models to gain insights. Models can integrate the existing data and incorporate key system-specific biological processes to provide a formal framework for understanding the mechanisms that drive the population biology of the system. Ecological systems are often nonlinear, and intuition in the absence of formal models may let us down as it did in the case of the squirrel system. In contrast, another good example of the use of a model in this context is that of Hoogendoorn & Heimpel (2002) that suggests that the invasive ladybird beetle actually reduces disease in a more susceptible native as it acts as a sink for a shared parasitoid. This again emphasises the importance of using models to understand these complex nonlinear interactions: it is not enough to show that there is a shared disease between competitors to show that there is a DMI.

Perhaps more controversial than whether models are useful in understanding ecological systems is what type of model is most appropriate. The invasion of the grey squirrel and the role of disease in this invasion provide an interesting case study to examine this. The first significant squirrel competition model was developed by one of the founders of mathematical ecology (Okubo *et al*. 1989). This model uses reaction-diffusion equations to examine

the spread of the grey squirrel assuming that there is only competition between reds and greys. The straightforward model framework and well-defined assumptions of this type of model provide very clear predictions that are easy to replicate or extend to other systems. An alternative approach was taken in the early 1990s where individual based models were used to examine the same problem (Rushton *et al.* 1997) leading to broadly similar conclusions. In these models, simulations are used where individual squirrels are modelled explicitly, and the population outcomes result from rule-based algorithms that are overlaid on a realistic spatial habitat (developed using GIS). This allows considerable complexity to be included in the model and can include rules to represent detailed behaviour and life-history patterns. These models have predictive power, but it is difficult to isolate the key drivers of the population dynamics due to the complicated choice of rules and large number of parameters. Nevertheless, because more of the biological complexity that is known to exist in the real system can be included in these rule-based approaches, they are widely used. The first model that included disease and competition was an extension of these individual rule-based models (Rushton *et al.* 1997, 2000). The conclusion of this model was that either disease alone or competition alone could account for the replacement of red squirrels with the combined action of competition and disease only having a small additional effect. In contrast, the second model that considered the role of disease and competition in the squirrel system (Tompkins *et al.* 2002) used a system of ordinary differential equations to represent the dynamics within a spatial patch (i.e. it assumed populations were spatially mixed at the patch level) and linked patches by dispersal. This model suggested that the disease in combination with competition was critical in explaining the speed of replacement that was seen in field observations. A question therefore is what it is about the assumptions of the two models that can explain this difference in inference. However, the difficulty in determining the key drivers of the population behaviour in complex rule-based systems makes this comparison problematic.

While including additional biological detail in model frameworks can be important, it should not be the overriding aim of a model. Indeed in its extreme, we can start with a real system that we do not understand and build a model that has a similar level of complexity to the real system that we also do not understand. The complexity of the model should depend on our understanding of the biological processes and the amount of data available. Often there is not enough data to appropriately simulate the system; rather, the aim should be to use data and models to gain an insight into the processes that are at play in the system. For example, theoretical work using simple general but spatially implicit models (Bell *et al.* 2009) makes the clear prediction that the disease is likely to spread in advance of the wave of grey squirrels and therefore impact on red abundance in the absence of greys (or following the removal of greys). Evidence of disease outbreaks in red strongholds (priority regions that support red populations) supports this finding and results in high mortality of reds and therefore increases the local extinction threat (Bruemmer *et al.* 2010). The observation that outbreaks occur in the red-only populations could be interpreted as evidence for the grey squirrel being less important than previously thought, but the modelling makes it clear that the observation is what we expect if the system is a spillover DMI. We argue that the best approach is to build appropriate simple models initially in order to gain insight into the role of different processes in the system and then build on this understanding with more complex models if we want to make predictions concerning management interventions.

Future directions

Many of the examples of DMIs that we have reviewed and in particular the red/grey/squirrelpox system in the UK are characterized by dramatic extinctions, invasions, epidemics or combinations of all three. Although these well-publicized cases illustrate the concept well, more subtle cases may have gone unnoticed, and therefore, the phenomenon may be much more common than we currently think. Without a comprehensive understanding of how all generalist parasites will interact with their hosts, we cannot hope to identify all DMIs before they occur. However, we can recognize and interpret patterns from known DMIs and use this knowledge to inform management decisions. For instance, we know that the fungus *Geomyces destructans* (*Gd*) causes white-nose syndrome (WNS) in North American bats and that it has already killed millions of bats in the north-eastern United States and Canada since 2006 (Turner *et al.* 2011). We also know that this virulent *Gd* strain appears to have been introduced from Europe (Warnecke *et al.* 2012), where *Gd* has been isolated from bats in eight countries, none of which have experienced WNS-associated bat declines (Puechmaille *et al.* 2011). We therefore strongly advise against any introduction of European bat species into North America, for fear of increasing the spread of WNS, accelerating the extinction of local bat species and/or facilitating a replacement of native bat species with invasive European bat species.

In terms of modelling, there is considerable potential to develop the theory on the importance and characteristics of DMIs. If the aim is to make conservation and management predictions, it will be necessary to include additional biological realism in models. In particular because initial invasions/infection levels occur at low density, it is essential to account for the stochastic nature of the dynamics as this may lead to disease fade-out or unsuccessful invasion attempts and can better reflect the population behaviour of natural systems. Moreover, it may be important to include key system-specific life-history properties. Additional realism in the form of seasonality, age structure, environmental variability and system-specific representations of transmission and immunity have been shown to be

important drivers of the population and epidemiological dynamics in single host–parasite systems (Altizer *et al*. 2006; Earn *et al*. 2000; Childs & Boots 2010; Keeling & Rohani 2008; Tompkins *et al*. 2011). Therefore, an understanding of their role in shared disease systems is urgent. This type of model is likely to fall between the deterministic and rule-based approaches that have been applied to the red/grey squirrel system and will need to provide a realistic representation of invasive spread and success, in which the key mechanisms that drive the dynamics can be understood. These approaches have great potential to be used to develop conservation and management strategies to protect native species from the threat caused by disease-carrying invaders.

Conclusions

We have reviewed a number of cases where disease-mediated processes have been implicated in invasions and conclude that (i) DMIs are a widespread phenomenon, that (ii) spillover is more common in animal invasions and spillback more common among plant invasions and that (iii) spillover DMIs are particularly important in explaining the replacement of native animals with phylogenetically similar exotic species. We have argued that detailed modelling of the type used in the grey squirrel invasion (Tompkins *et al*. 2003) is a useful approach to gain an understanding in which of these specific examples the disease is likely to be or have been important. Even in cases where the amount of empirical data is limited simple models can give at least an indication of the circumstances under which the disease may have been important. Furthermore, they can inform on the most important pieces of data to collect in order to better understand the invasive process. Another important question is whether there are particular evolutionary consequences of DMIs. On one level, it is clear that native organisms will be selected for higher resistance or tolerance (Boots *et al*. 2009) in the face of the DMI. However, it is unclear whether the characteristics of DMIs are more or less likely to allow the evolution of defence, and therefore, we need evolutionary models that include the particular epidemiological feedbacks intrinsic to DMIs. Taken as a whole, the question of DMI warrants further study: it may prove to be a major force in the invasion of non-indigenous species.

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