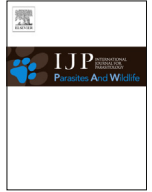




Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Invited Review

Co-invaders: The effects of alien parasites on native hosts



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ARTICLE INFO

Article history:

Received 20 November 2013

Revised 9 April 2014

Accepted 9 April 2014

Keywords:

Invasive species
Co-introduction
Co-invasion
Host-switching
Virulence

ABSTRACT

We define co-introduced parasites as those which have been transported with an alien host to a new locality, outside of their natural range, and co-invading parasites as those which have been co-introduced and then spread to new, native hosts. Of 98 published studies of co-introductions, over 50% of hosts were freshwater fishes and 49% of parasites were helminths. Although we would expect parasites with simple, direct life cycles to be much more likely to be introduced and establish in a new locality, a substantial proportion (36%) of co-introductions were of parasites with an indirect life cycle. Seventy-eight per cent of co-introduced parasites were found in native host species and can therefore be classed as co-invaders. Host switching was equally common among parasites with direct and indirect life cycles. The magnitude of the threat posed to native species by co-invaders will depend, among other things, on parasite virulence. In 16 cases where co-introduced parasites have switched to native hosts and information was available on relative virulence, 14 (85%) were more virulent in native hosts than in the co-introduced alien host. We argue that this does not necessarily support the naïve host theory that co-invading parasites will have greater pathogenic effects in native hosts with which they have no coevolutionary history, but may instead be a consequence of the greater likelihood for parasites with lower virulence in their natural host to be co-introduced.

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Contents

1. Introduction	171
2. Recognising alien parasites	173
3. Introduction and establishment of alien parasites	173
4. Host switching by alien parasites	174
5. Virulence of co-invaders to native hosts	174
6. Control of invaders and co-invaders	175
7. Conclusions	175
Acknowledgements	176
Appendix A. Supplementary data	176
References	176

1. Introduction

Invasive species are alien (non-native) organisms that have been introduced into an area outside of their natural range, established self-sustaining populations and spread beyond their initial point of introduction, with deleterious impacts on the

environment, the economy or human health (Kolar and Lodge, 2001). Human population growth, increasing transport capacity and economic globalisation have accelerated the rate of introductions of alien species throughout the world (Vitousek et al., 1997; Sakai et al., 2001). Invasive species are now recognised as a major cause of biodiversity loss and associated changes in ecosystem function, leading to biotic homogenisation as native species are replaced by widespread alien species (Pimentel, 2002; Rahel, 2002; Simberloff, 2011).

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There has been a dramatic growth in the study of biological invasions in the last twenty years, with a concomitant and confusing amplification of terminology (Falk-Petersen et al., 2006; Blackburn et al., 2011). Blackburn et al. (2011) proposed a unified framework for biological invasions that describes the status attained by alien species as they progress through a series of barriers in their new environment. In this framework, an alien species must surmount geographic barriers to be introduced into a new area, then barriers to survival and reproduction to become established within the expanded range, and finally barriers to dispersal to become invasive (Table 1; Fig. 1a). No specific terms have been proposed to distinguish alien species which adversely affect the environment, economy or human health from those which do not have adverse effects, but in practice the term “invasive” usually connotes negative impacts, particularly on the environment (Falk-Petersen et al., 2006).

Invasive species may affect native species directly, through competition or predation, or indirectly, by altering habitat or changing disease dynamics. Parasites may play a key role in mediating the impacts of biological invasions at any of the three phases of introduction, establishment or spread. Introduced alien hosts often have fewer parasite species and a lower prevalence of parasites than native hosts, which may provide them with a competitive advantage (enemy release; Mitchell and Power, 2003; Torchin et al., 2003). Once introduction has occurred, parasite transmission may occur from native hosts to alien hosts, leading to an increase in infection of natives if aliens amplify transmission (spillback; Kelly et al., 2009; Mastisky and Veres, 2010) or a decrease in infection of natives if aliens reduce transmission (dilution; Paterson et al., 2011; Poulin et al., 2011). If alien hosts introduce new parasites, then these may be transmitted to native hosts, leading to the emergence of new disease in the natives (spillover or pathogen pollution; Daszak et al., 2000; Taraschewski, 2006).

To threaten native hosts in a new locality, alien parasites must overcome the same barriers to introduction, establishment and spread as free-living aliens and, in addition, they must be able to switch from alien to native hosts. We propose using the terminology of co-introduced for those parasites which have entered a new area outside of their native range with an alien host, and co-invader for those parasites which have been co-introduced and then switched to native hosts (Table 1; Fig. 1b). It does not seem useful to make a distinction between introduced and established alien parasites, in the same way that this distinction is made for free-living aliens, because, except in very special circumstances (e.g., MacLeod et al., 2010), introduced parasites which do not establish are unlikely to ever be recorded. Similarly, we see little value in distinguishing between alien parasites in established alien hosts and those in invasive alien hosts if they have not switched to native

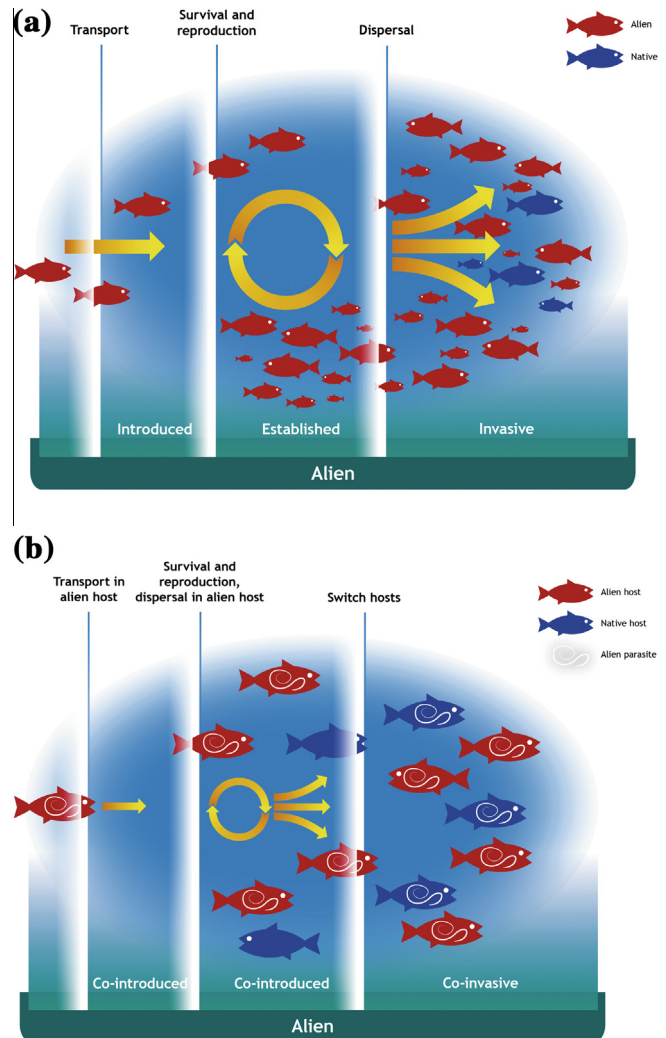


Fig. 1. Schematic diagram of processes involved in species invasions and co-invasions. (a) Free-living aliens. The light blue oval shape represents a new area, outside the natural range of the alien species, shown in red. Arrows indicate movement of alien species through the phases of introduction, establishment and invasion of the habitat of the native species, shown in blue. Vertical bars represent barriers to be overcome in each phase. (b) Parasitic aliens. The alien host species (in red) contains an alien parasite species. The alien parasite goes through the processes of introduction, establishment and spread with its original host and then switches to a native host species (in blue) to become a co-invader. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Terminology for alien host and parasite species.

Term	Definition
Native species	A species occurring within the range it occupies (or could occupy) naturally, independent of human activity
Alien (exotic, non-indigenous) species	A species that has been transported by human activity into an area outside its natural range
Introduced species	Alien species that has been transported by humans into an area outside its natural range, but has not yet established self-sustaining populations in the wild
Established (naturalised) species	Alien species that has been introduced and established self-sustaining populations in the wild
Feral species	Alien species that has been kept in captivity or domestication after introduction, but has escaped or been released to establish self-sustaining populations in the wild
Invasive species	Alien species that has been introduced, become established and is expanding its range, usually with deleterious consequences for native species
Co-introduced parasite	An alien parasite species that has been transported into a new area with an alien host species
Co-invasive parasite	A co-introduced parasite species that has infected native host species in the new range

hosts, as this is the crucial step in parasites adversely impacting the new environment. Although co-invading parasites are often considered to be important causes of disease emergence, producing high morbidity and mortality in native hosts (Taraschewski, 2006; Peeler et al., 2011), the extent to which co-introduction and co-invasion occur and the magnitude of the threat posed to native species have not been well documented (Smith and Carpenter, 2006). In this paper we will review previous studies on co-introduced parasites, examine the characteristics associated with host switching and compare the relative pathogenicity of co-invaders to native and alien hosts.

2. Recognising alien parasites

It is not always straightforward to determine whether a newly discovered parasite is alien or native to a region. Cryptogenic species, those that are not demonstrably alien or native, appear to be remarkably common in terrestrial, freshwater and marine ecosystems (Carlton, 1996). This is partly because human-mediated transport of organisms began long before taxonomic surveys and species monitoring programs, and partly because many species, particularly of parasites, are difficult to identify or have ambiguous taxonomies (Thomsen et al., 2010).

For cryptogenic species, there are a number of historical, biogeographic, genetic, taxonomic and ecological criteria that can be used to determine alien or native status. Chapman et al. (2012), for example, inferred that the parasitic isopod *Orthione griffenis*, which infects mud shrimps, had been introduced to North American coastal waters based on its conspecificity with disjunct Asian populations, earliest collections in Asia, late discovery in North America, and appearance coincident with extensive ballast water traffic from Asia. Gaither et al. (2013) inferred the introduced status of the nematode *Spirocamallanus istiblenni* in native and cultured alien fishes in Hawaii through its phylogenetic similarity to a disjunct lineage in French Polynesia, low genetic diversity, indicating a founder effect, and a lag between alien host and parasite geographic distribution in Hawaii.

3. Introduction and establishment of alien parasites

Parasites may occasionally be introduced into a new locality without their host(s). For example, it is likely that free swimming stages of the isopod *O. griffenis* were transported in ballast water to North America (Chapman et al., 2012). Similarly, eggs and juveniles of the swimbladder nematode *Anguillicola crassus*, a parasite of the Japanese eel *Anguilla japonica*, were introduced by aquaculture transport vehicles into the United Kingdom, where they have successfully parasitised native European eels, *Anguilla anguilla* (Kirk, 2003). Alien parasites may also be introduced with native hosts, if those hosts have been translocated, acquired infection with a new parasite species and then been re-introduced into their original habitat. For example, the natural host of the parasitic brood mite *Varroa destructor* is the Asian bee *Apis cerana*. The European honeybee *Apis mellifera* acquired the mite when it was introduced to Asia early in the 20th century. Although the details are unclear, it appears likely that the mite was then introduced into Europe with infested European honeybees, rather than with the alien Asian bee (Oldroyd, 1999; Anderson and Trueman, 2000).

Most alien parasites, however, are co-introduced with an alien host species. A literature survey identified 98 examples of co-introductions of alien hosts and parasites, across a wide range of taxa (Fig. 2; Supplementary data, Table S1). The most common co-introduced parasites found in published studies were helminths, making up almost 49% of the total, with arthropods at 17% and protozoans at 14% (Fig. 2a). This is likely to reflect, at least

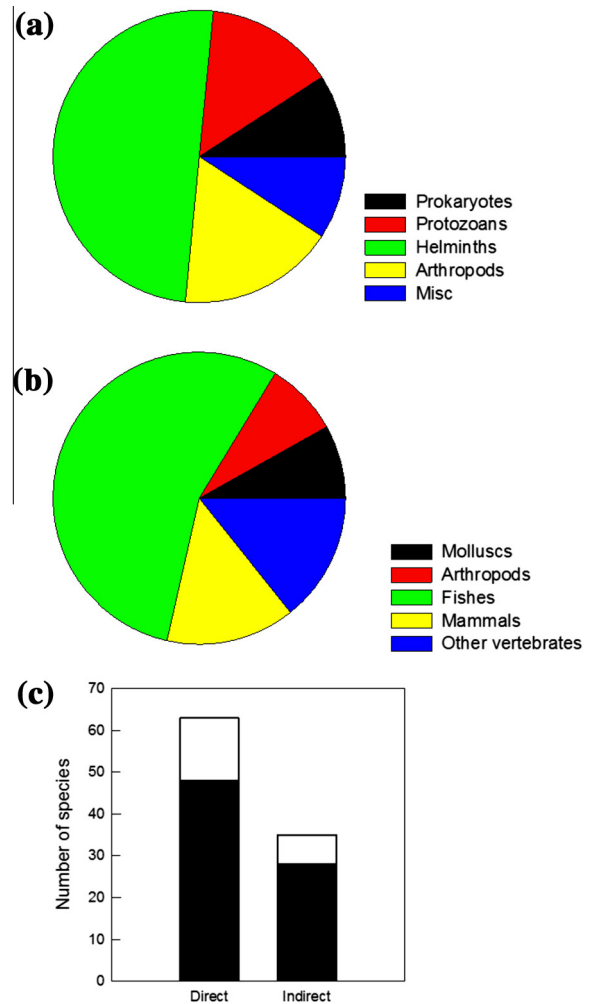


Fig. 2. (a) Relative proportions of taxa represented in 98 examples of co-introduced parasites: prokaryotes (viruses and bacteria); protozoans; helminths (platyhelminths, nematodes and acanthocephalans); arthropods (crustaceans, arachnids); and a miscellaneous group including fungi, myxozoans, annelids, molluscs and pentasomids. (b) Relative proportions of alien hosts represented in 98 examples of co-introductions: molluscs; arthropods; fishes; mammals; and other vertebrates (amphibians, reptiles and birds). (c) Number of co-introduced parasite species with direct and indirect life cycles which have switched (black bars) or not switched (white bars) from alien to native host species.

in part, our selection criteria for studies that had good evidence for parasite co-introduction with an alien host. Although viral and bacterial microparasites are generally considered to be much more important than macroparasites as emerging pathogens in wildlife, in many cases their origin is unclear (Daszak et al., 2000; Dobson and Foufopoulos, 2001) and they made up only 9% of parasite co-introductions that we found. Fishes were by far the most common alien hosts in published studies, making up 55% of the total (Fig. 2b), with 81% of fish hosts being either freshwater or diadromous. This may reflect a taxonomic bias in studies, but is also likely due to the propensity for freshwater ecosystems to be particularly affected by invasive fishes (García-Berthou, 2007; Johnson and Paull, 2011).

It is now well established that introduced alien species usually harbour significantly fewer parasites than native species (Mitchell and Power, 2003; Torchin et al., 2003; Lymbery et al., 2010; Roche et al., 2010). This may arise because founding populations of aliens do not carry the complete range of parasites found in the source location or because co-introduced parasites are unable to complete their life cycle (i.e., to establish) in the new environment. Ewen

et al. (2012) found that avian malaria parasites (*Plasmodium* spp.) that have successfully invaded New Zealand are more prevalent in their native range than related species of *Plasmodium* that have not invaded, and Torchin et al. (2003) reported similar findings across a range of host and parasite taxa. This may argue in favour of the importance of arrival with the host, as a higher prevalence means a greater probability of being present in host founders (Ewen et al., 2012), but a higher prevalence may also indicate a greater transmission efficiency and therefore a greater ability to persist in the new environment. Distinguishing between these two processes is not usually possible because data on host and parasite founding populations are lacking. MacLeod et al. (2010) used a host/parasite system for which such data were available – chewing lice on introduced birds in New Zealand – and found that failure to persist in the new environment was a much more important source of loss of parasite species than was failure to arrive with their hosts.

It is usually considered that the establishment of parasites in a new environment is much more likely to occur in those species with simple, direct life cycles (vertical transmission or horizontal transmission without the need for intermediate hosts; Dobson and May, 1986; Bauer, 1991; Torchin and Mitchell, 2004). Dobson and May (1986), for example, suggest an order of magnitude difference in the establishment of directly transmitted parasites compared to those with an indirect life cycle. There have been no empirical tests, however, of this hypothesis, because of the difficulty in obtaining data on parasite founding populations, prior to establishment. Mitchell and Power (2003) found that invasive plant species had proportionally more viral than fungal co-introductions (24% fewer viruses and 84% fewer fungi than in their natural range) and suggested that this reflects, in part, a greater tendency for viruses to be seed-transmitted. In the 98 examples of parasite co-introductions in Table S1, 64% of parasites had a direct life cycle and 36% had an indirect life cycle (Fig. 2c). This suggests that parasites with a direct life cycle might establish more readily in a new environment, but it is not a proper test of the hypothesis because we have no data on parasite co-introductions which failed to establish. The data are also affected by a taxonomic bias. Twenty-two of the parasites (22.4%) were monogeneans, all of which have a direct life cycle. If these are excluded, then the ratio for published examples of co-introductions becomes 54% with a direct life cycle and 46% with an indirect life cycle.

For co-introduced parasites with an indirect life cycle, successful establishment requires an alternative host which is already present in the recipient locality. For example, native copepods can act as intermediate hosts for the introduced nematode *S. istiblenni*, infecting fishes in Hawaii (Gaither et al., 2013), and native dragonflies and damselflies are intermediate hosts for the introduced trematode *Haematoloechus longiplexus* in American bullfrogs (*Lithobates catesbeianus*) on Vancouver Island, Canada (Novak and Goater, 2013). The surprising aspect from published studies is the frequency with which co-introduced parasites with indirect life cycles can establish in the new environment, with examples of successful co-introductions in protozoan, myxozoan, trematode, cestode, nematode, acanthocephalan and pentastomid parasites.

4. Host switching by alien parasites

Parasites which are co-introduced with their hosts may establish and spread geographically in their new range with their original, alien host, without switching to native hosts. Although 78% of the 98 examples of co-introduced parasites in Table S1 were recorded in native hosts (i.e., became co-invaders), this is likely to overestimate the real incidence of host-switching, as null studies are generally less likely to be reported (Arnqvist and Wooster,

1995). Co-introduction without host-switching has been found, for example, in monogenean parasites of invasive pumpkinseed fish (*Lepomis gibbosus*) in the Danube River Basin, Central Europe (Ondrackova et al., 2011), the lungworm *Rhabdias pseudosphaerocephala* in cane toads (*Rhinella marina*) in Australia (Pizzatto et al., 2012), and the trematode *H. longiplexus* in American bullfrogs in Canada (Novak and Goater, 2013).

We found no evidence from published studies of an effect of life cycle on host switching. Of the 98 parasite co-introductions in Table S1, 76.2% of parasites with a direct life cycle, and 80.0% of parasites with an indirect life cycle successfully switched to native hosts (Fig. 2c). This does not represent a particularly strong test of the influence of life cycle on propensity to switch hosts, because it does not control for parasite or host phylogeny or for many of the other factors which may influence the propensity for host-switching to occur. These factors include host specificity and the similarity of host fauna and environmental conditions between source and recipient localities (Bauer, 1991; Kennedy, 1993). Nevertheless, it appears that not only are many parasites with complex, indirect life cycles able to be co-introduced and establish readily in a new environment, they are also no less likely to infect native hosts and become co-invasive than are parasites with direct life cycles.

5. Virulence of co-invaders to native hosts

Of the 76 examples of co-introduced parasites that switched to native hosts, we were able to obtain information on relative virulence in 16 of them, from estimates of pathogenic effects in either naturally or experimentally infected hosts. Of these 16 parasites, 14 (85%) were more virulent in native hosts than in the co-introduced alien host, while for the other two, there was no evidence of any difference in virulence between native and alien hosts. The effect of the swim-bladder nematode *A. crassus* on the Japanese eel (*A. japonica*) and the European eel (*A. anguilla*), provides a clear example of increased virulence in native, compared to alien hosts. *A. crassus* is a common parasite of Japanese eels in east Asia, but is generally found at low intensities, with no obvious adverse effects on the swim-bladder or the general condition of infected eels (Nagasawa et al., 1994). The parasite was introduced to Europe with imported Japanese eels in the 1980's and successfully colonised European eels (Kirk, 2003). Worm intensities are typically greater in naturally infected European eels than in Japanese eels, and infection is associated with enlargement of the swim-bladder, thickening and fibrosis of the swim-bladder wall, haemorrhage, secondary bacterial infections and acute and chronic inflammatory responses (Kirk, 2003). Infected European eels have reduced appetite and poor body condition (Nagasawa et al., 1994). Knopf and Mahnke (2004) experimentally infected eels with *A. crassus* larvae and found that, compared to Japanese eels, worms in European eels had significantly greater survival rate and faster development, leading to a greater adult worm burden.

It has been proposed that parasites which switch from introduced host species to native host species will have greater pathogenic effects in native hosts, with which they have no coevolutionary history (naïve host syndrome, Mastitsky et al., 2010; novel weapon hypothesis, Fassbinder-Orth et al., 2013). The coevolution of parasites and their hosts is often viewed as a contest between parasite virulence (parasite-induced reduction in host fitness; Combes, 2001) and host resistance (ability to prevent infection) or tolerance (ability to limit the damaging effects of infection) (Best et al., 2008; Svensson and Råberg, 2010). The naïve host theory is that parasites and hosts with a long coevolutionary history will be co-adapted; when alien parasites are introduced to a new area they meet naïve hosts which lack coevolved

resistance or tolerance, and therefore are more likely to become infected and/or to suffer greater pathogenic consequences from infection (Allison, 1982; Mastitsky et al., 2010; Fassbinder-Orth et al., 2013).

Although the naïve host theory appears to be implicit in many discussions of the impacts of co-invading parasites on native hosts (e.g., Daszak et al., 2000; Prenter et al., 2004; Peeler and Feist, 2011; Peeler et al., 2011; Britton et al., 2011a), there are at least two reasons why it should be viewed sceptically. First, we often cannot assume a coevolutionary relationship between a parasite and the alien host with which it is introduced, particularly for widespread alien hosts which may have acquired the parasite relatively recently (Taraschewski, 2006). Second, and more importantly, there is no *a priori* reason to expect the consequences of infection to be more severe in immunologically naïve host species, than in host species with which the parasite has coevolved. Because parasites generally have larger population sizes and shorter generation times than their hosts, they are expected to be ahead in the coevolutionary arms race and therefore to have greater mean fitness in local than in foreign host populations (Kaltz and Shykoff, 1998; Dunn, 2009). Parasite fitness, however, may be enhanced either by increased or decreased virulence, depending on the circumstances of transmission (May and Anderson, 1983; Ebert and Herre, 1996). Indeed, if the new host is not phylogenetically closely related to the coevolved host, then any level of virulence might result, because virulence expressed in an unusual host will not necessarily relate to parasite fitness (Ebert, 1995).

Nevertheless, co-invading parasites may exhibit greater virulence to new, native hosts than to the alien hosts with which they were introduced, simply by chance. The probability of introduced hosts surviving the translocation process is likely to be inversely related to the virulence of any parasites they carry into their new range, because most introductions involve a few individuals being transported over difficult geographic barriers or escaping from captivity (Blackburn et al., 2011). As a consequence, parasites with lower virulence in their natural host will be much more likely to be co-introduced (Strauss et al., 2012). If virulence of the parasite differs between the coevolved alien host and the new, native host, it is therefore more likely to be in the direction of increased virulence in the new host.

The introduction and spread of a new, virulent parasite may have catastrophic effects on native host populations. Both theoretical and empirical studies have demonstrated that parasites can provide density dependent regulation of their host populations through effects on host mortality and fecundity rates (Anderson and May, 1992; McCallum and Dobson, 1995; Hudson et al., 1998). If the parasite is relatively avirulent in the co-invading alien host, then this host can act as a reservoir of infection for native hosts, even as their populations decline (McCallum and Dobson, 1995; Daszak et al., 2000; Holt et al., 2003).

There are, unfortunately, many apparent examples of this phenomenon. On the International Union for Conservation of Nature list of the world's worst invasive species, infectious disease is the main driver behind the impact of invasion in almost 25% of cases (Hatcher et al., 2012). In many instances, these diseases are caused by co-introduced parasites that have switched from alien to native hosts. *Plasmodium relictum* (causing avian malaria), for example, was introduced to Hawaii with alien birds (and the primary mosquito vector, *Culex quinquefasciatus*) in the early 20th century. Native bird species are much more susceptible than alien species, suffering mortality rates of 65–90%, contributing to the extinction of almost half of the endemic bird fauna of Hawaii (Warner, 1968; Woodworth et al., 2005). Squirrel parapoxvirus (Chordopoxviridae; uncertain taxonomic status) is likely to have been introduced into the UK with grey squirrels (*Sciurus carolinensis*) from North

America. The virus has no clinical effects on grey squirrels, but can also infect red squirrels (*Sciurus vulgaris*), causing high mortality rates and a decline in red squirrel populations (Tompkins et al., 2003; Rushton et al., 2006). Crayfish plague, caused by the fungus *Aphanomyces astaci*, has caused dramatic population declines in freshwater crayfish species throughout the world (Holdich and Reeve, 1991; Söderhäll and Cerenius, 1999; Evans and Edgerton, 2002). The parasite is largely asymptomatic in its natural North American freshwater crayfish hosts, but when spread with these hosts (or with ballast water or fish vectors) to new localities, has proved to be virulent in many European, Asian and Australian crayfish species (Holdich and Reeve, 1991; Söderhäll and Cerenius, 1999; Evans and Edgerton, 2002).

6. Control of invaders and co-invaders

Invasive species are recognised as a major threat to biodiversity and much effort is extended in their control (Hauser and McCarthy, 2009; Sharp et al., 2011; Britton et al., 2011b). The intended outcome of such control programs is the recovery of native species or ecosystems, although control of invasive species may have unintended consequences that prevent this outcome being realised (e.g., Bergstrom et al., 2009; Walsh et al., 2012). The effect of control programs on co-invading parasites has rarely been considered, but should be included in risk assessments prior to management interventions to control invasive species, because both invasive hosts and their co-invading parasites may fundamentally alter ecosystem function (Roy and Lawson Handley, 2012; Amundsen et al., 2013).

In standard models of microparasite population dynamics, transmission rate is inversely related to virulence (Anderson and May, 1992), so we should expect that if introduced parasites are usually more virulent in native hosts, then alien hosts will act as reservoirs of infection, amplifying the effects of the parasite in native hosts. This seems to have occurred, for example, with avian malaria in Hawaii, the squirrel poxvirus in the UK and crayfish plague throughout Europe, where the natural, alien hosts increased transmission to native hosts (Dunn, 2009; Hatcher et al., 2012). If invasive aliens are more competent to transmit infections than native species for a co-invading parasite, then control of the alien will reduce the infection pressure on native hosts.

The situation may not be so straightforward for many macro-parasites, however. The expected inverse relationship between virulence and transmission rate arises from a simple mass action model of transmission, where transmission rate depends on the numbers (or densities) of infected and susceptible hosts, and increasing virulence removes infected hosts from the population (McCallum et al., 2001). In reality, the transmission process is likely to be much more complicated, particularly for parasites with complex life cycles, and there is limited theoretical or empirical support for a general trade-off between virulence and transmission rate (Ebert and Bull, 2003). Alien hosts, therefore, may not always act as amplifying reservoirs, even when the parasite is less virulent in them than in native hosts. If invasive aliens are less competent to transmit infections than native hosts, then control of the alien may inadvertently amplify infection of natives. Whether this is likely to constitute a real problem for the control of alien species is not known, because there are very few empirical data on the relative competencies of different hosts for the transmission of any multi-host parasites (Haydon et al., 2002), let alone for alien and native hosts in transmitting co-invading parasites.

7. Conclusions

It appears from published studies that co-introductions of parasites with alien hosts occur over a wide range of parasite and host

taxa and often involve parasites with complex life cycles that require an alternative host in the new locality. Parasites of freshwater fishes are particularly well represented in the literature and this may reflect the susceptibility of freshwater environments to alien introductions. Once established, infection of native hosts is common and, from the limited data available, virulence is usually greater in native hosts than in the alien host with which the parasite was introduced. Successful control of the alien host may reduce the impact of the parasite on the native host population, if lower virulence in the alien host is associated with greater transmission efficiency, but we have little information on this point.

Acknowledgements

This work was funded by the Australia and Pacific Science Foundation and an Australian Postgraduate Award to Mikayla Morine. Thanks to Mark Preston of Murdoch Design for the species invasion diagram (Fig. 1). The authors have no conflicts of interest to disclose.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ijppaw.2014.04.002>.

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