Table 1: Examples of direct and indirect effects of parasites in biological invasions.

Host(s)–Parasite(s) system	Direct effect of parasite on the host(s)	Indirect effect and wider impact	Example citation
Parasite mediated competition			
H: Invasive grey squirrel *Sciurus carolinensis* and native red squirrel, *S. vulgaris* P: Invasive Pox virus	Parasite is of low virulence to invader, but high virulence to native species	Parasite spills-over into red squirrels causing high mortality. Theoretical models predict increased competitive replacement of reds	Tompkins White & Boots 2003;
H: Invasive Asian cyprinid fish, *Pseudorasbora parva* and native cyprinid *Leucaspius delineatus* P: Invasive intracellular eukaryote	Parasite is of low virulence to the invader, but high virulence to native species	Spillover of parasite from invader causes high mortality in native species thereby reducing ability of native fish to compete with invader, facilitating invasion success	Gozlan et al. 2005

H: Invasive variegated leafhopper *Erythroneura variabilis* and native grape leafhopper *E. elegantula.* P: Native parasitoid *Anagrus epos*	Native leafhopper experiences higher attack rates from the shared parasitoid (*A. epos)* than does the invader	Differential parasitism rates shifts competitive balance in favour of the invader.	Settle & Wilson 1990
H: Invasive trout, *Salmo trutta* and native *Galaxias* fish. P: Native trematode parasites, e.g., *Gobiomorphus breviceps* Stokell and *Galaxias anomalus*	Native *Galaxias* fish suffer increased exposure to trematode parasites	Invasive tout displaces native *Galaxias* into low flow, higher temperature refuges, thereby increasing trematode exposure	Poulin et al. 2011
H: Invasive Mediterranean marine mussel *Mytilus galloprovincialis* and native mussel *Perna perna* P: Two trematode species	Parasites have sub-lethal effects; one parasite causing reduced host growth whilst the second causes castration, reduced adductor muscle strength and water loss	Parasites reduce the ability of the native mussel to compete with the invader (which remains uninfected), and may contribute to the invasion success of the Mediterranean mussel	Calvo-Ugarteburu & McQuiad 1998

H: Invasive ant *Solenopsis invicta* and native ant *S. geminata* P:Native phorid parasitoid *Pseudacton browni*	Native ant adopts defensive behaviors in presence of parasitoid. Invasive ant less affected	A greater decline (50%) in foraging rates of native ant compared with invasive shifts competitive balance in favor of invasive ant facilitating invasion success	Morrison 1999
H: Invasive ant *Solenopsis invicta* and native ant *Forelius mccooki* P:Invasive phorid parasitoid *Pseudacton tricuspis*	Invasive ant adopts defensive behaviors in presence of parasitoid. Native ants not affected	A decline in foraging rates of invasive ants reduces the invaders ability to compete with the native ant. Used in biological control	Mehidiabadi, Kawazoe & Gilbert 2004
H: Native European pines and introduced eastern white pine, *Pinus strobes*. P: Native blister rust *Cronartium ribicola*	Rust is sustained by the indigenous species but is more virulent to the introduced species	Introductions into Europe have failed because of biotic resistance (attacks) by native rust.	Harper 1977; Mangla, Inderjit & Callaway 2008
H: Invasive annual and native perennial grasses P: Barley and cereal Yellow Dwarf viruses	Infected native species experience more severe reduction of growth than invasives	Ability of natives to compete against invasives is reduced. Viruses may have contributed to replacement of perennial grasslands by invasive annuals	Malmstrom et al. 2005; Borer et al. 2007

H: Invasive weed, *Chromolaena odorata* and native plants P: Fungal pathogen, *Fusarium semitectum*	Growth of native plants is reduced by the fungal pathogen	Fungal pathogen accumulates on the roots of the invasive weed, increasing the number of infectious propagules in the environment	Mangla, Inderjit & Callaway 2008
H: Invasive grass, *Bromus tectorum* and five species of native grass P: Fungus *Pyrenophora semeniperda*	Seeds of the invasive act as a reservoir for pathogen. Seeds of native grasses suffer 10-90% mortality	Seeds of natives more likely to be killed in *B. tectorum* dominated patches. May contribute to ability of *B. tectorum* to displace native grasses on a landscape scale	Beckstead et al. 2010
H: Invasive grass, *Lolium arundinaceum* and native trees P: Endohpyte, *Neotyphodium coenophialum*	Endophyte-infected grasses are toxic to herbivores, suppress native tree growth	Native tree growth reduced in presence of infected grasses. Endophyte-infected grasses may suppress or alter succession	Rudgers et al. 2007
H: Invasive forb, *Centaurea maculosa* and native grass *Festuca idahoensis* P: mycorrhizal fungi	No direct effect of mycorrhizae on *C. maculosa* of *F. idahoensis*	Mycorrhizae increase growth of *C. maculosa*, decrease growth of *F. idahoensis* only, when grown together. May help *C. maculosa* to outcompete native grasses	Marler et al. 1999

H: Invasive Garlic Mustard *Allaria petiolata* and native tree seedlings P: mycorrhizal fungi	Infected native tree seedlings have enhanced growth	Root exudates of invasive *A. petiolata* inhibit mycorrhizae of native species, reducing their performance. May contribute to invasiveness of *A. petiolata,* impacts on native forest plants	Stinson et al. 2006
Apparent competition			
H: Native UK grey partridge *Perdix perdix* and managed pheasants *Phasianus colchicus* *P:* Nematode, *Heterakis gallinarum*	Parasite is more virulent in native grey partridge than in managed pheasants. Declines in grey partridge may be due to effect of parasite on the host.	Apparent competition between pheasants and grey partridge mediated by the nematode. Some interspecific completion is also likely to occur.	Tompkins et al. 2000
H: Invasive American bullfrog *Rana catesbeiana* and native amphibian species P: fungus *Batrachochytrium dendrobatidis*	Parasite is of low virulence to the invader, but causes high mortality in native species	Fungus has become ubiquitous and is posited to be a driver in global amphibian declines. Environmental factors (temperature and precipitation) further exacerbates the impact.	Reviewed in Hatcher and Dunn 2011; Lips et al. 2008
Parasites of resource organisms			

H: Invasive gypsy moth *Lymantria dispar* P: Native baculovirus	Baculovirus causes mortality once population reaches a critical community size	Predators regulate moth densities. When predator is satiated, pathogens become a regulatory force on invasive species. Combined effects of pathogens and predators help to regulate outbreaks of invader	Dwyer, Dushoff & Yee 2004
H: European rabbit *Oryctolagus cuniculus* P: Invasive rabbit haemorrhagic disease virus	Widespread decline in European wild rabbit population	Loss of keystone prey species (rabbit) led to near extinction of two endangered top predators: Iberian Lynx (*Lynx pardinus*) & imperial eagle (*Aquila adalberti*)	Ferrer & Negro 2004
H: Native tree, *Castanea dentate* and Lepidopteran species P: Invasive fungus, *Cryphonectria parasitica*	Invasive parasitic fungus devastated populations of American Chestnut	Loss of hosts for native specialist herbivores. Several specialist lepidoptera are believed to have become extinct as a result	Dunn 2005
H: Invasive grass *Andropogon bladhii* and native grass. *A. gerardii* P: Fungal infections, including *Gaeumannomyces graminis*	Infection causes mortality in grasses. Seeds are not produced in the heads of infected plants	Nitrogen fertilization increased fungal infection in the native grass *A. gerardii*, but not its invasive congener A. bladhii.	Han et al. 2008

H: Native whelk *Nucella lapillus* P: Native spionid polychaete worm (*Polydora* sp.)	Polychaete weakens the structural integrity of native whelks' shells	Invasive green crabs (*Carcinus maenas*) prey on large infected whelks that have weakened shells that were formerly not predated by crabs. Infection broadens range of susceptible prey, increasing ecological impact and success of invasion	Fisher 2010
P: seed boring parasite (spp. Unknown) H: Broad-leaved tree species	Parasite structurally modifies tree fruits	Modification by parasite allows invasive dipteran *Chymomyza amoena* to oviposit in fruit. Increase in geographical distribution of invasive dipteran	Band, Bachli & Band 2005
H: Invasive yellow starthistle *Centaurea solstitialis* P: Introduced fungus *Puccinia jaceae f.s. solstitialis*	Infection by fungus influenced plant quality / defense	Infection by fungus increased impact of bud-feeding by adult weevils, but reduced impact of seed-feeding by larval weevils. Synergy and interference between enemies of invasive plants may affect efficacy of biocontrol agents	Swope and Parker 2010

H: Native American beech *Fagus grandifolia* P: Invasive beech bark disease *Neonectria* spp.	Invasive scale insect *Cryptococcus fagisuga* attacks tree, causing mechanical damage	Damage on tree facilitates fungal infection by invasive beech bark disease. On-going population decline of American beech.	Kenis et al. 2009
H: Native Elm tree *Ulmus americana* P: Invasive fungi *Ophiostoma ulmi* & *O. novo-ulmi*	Invasive bark beetle *Scolytus multistriatus* burrows into elm tree, transports fungi	Burrowing into elm tree by beetle transmits fungal infections causing Dutch elm disease. Significant (>50%) losses of elm trees in North America by Dutch elm disease leads to broad changes in forest community structure and composition	Kenis et al. 2009
H: Invasive spurge *Euphorbia esula* P: Fungi, *Rhizoctonia solani* & *Fusarium oxysporum*	Minor effect of fungal infection on invasive spurge	Significant increase in fungal damage in the presence of herbivore flea beetle (*Aphthona* spp.). Suppression of invasion by synergistic effect of herbivore and fungal parasite	Caesar 2003
Parasites of consumers			

H: Invasive Rabbit, *Oryctolagus cuniculus* P: Myxoma virus	Virus highly virulent to host following initial introduction of parasite causing dramatic population declines	Parasite-induced mortality in hosts reduced grazing pressure allowing regeneration of oaks (*Quercus robur*)	Dobson & Crawley 2004
H:Native wolves, *Canis lupus* P: Introduced canine parvovirus (CPV)	Causes mortality in infected wolves	Parasite-induced mortality of wolves reduces their regulatory impact on major prey item the moose (*Alces alces*) an effect that is potentially exacerbated in this closed population (Isle Royale, US)	Wilmers et al. 2006
H: Naturalized cattle and native wildebeest (*Connochaetes taurinus*) P: Invasive virus, rinderpest	High mortality in both naturalized cattle and native wildebeest	Effective removal of the parasite from cattle by vaccination halted spillover into wildebeest allowing the population to increase dramatically in size. The consequential increase in grazing ultimately may have led to a decline in fire and an increase in tree cover.	Holdo et al. 2009

H: Parsnip moth, *Depressaria sativa,* herbivore on the invasive parsnip (*Pastinaca sativa*) P: Parasitoid, *Copidosoma sosares*	Widespread infection of the moth by the parasitoid, suppresses the moth population density, reducing herbivory on the invasive parsnip.	Invasive parsnip reduces production of costly defences (furanocoumarin) in response to reduced herbivory, thereby potentially reallocating resources to fitness and facilitating invasion	Ode et al. 2004
H: Native amphipod *Gammarus duebeni celticus* and invasive amphipod predator *Gammarus pulex* P: Native acanthocephalan parasite *Echinorhynchus truttae*	Infected invasive *G. pulex* were more active and consumed 30% more prey than uninfected individuals	Increased foraging rates impacts its prey and its competitors. This is likely to exacerbate the impact of the invader on native invertebrate diversity and biomass	Kelly et al. 2006 Dick et al. 2010
H: Invasive Asian mud snails *Batillaria attramentaria* and native California horn snail, *Cerithidea californica* P:Invasive trematode *Cercaria batillariae*	Parasite induces castration, gigantism and increased foraging in invasive snails No effect on native snails	Increased feeding of infected snails may alter the impact of the invader both on its resources and on the native competitors	Byers 2000 Torchin 2005

H: Native white clawed crayfish (*Austropotamobius pallipes*) P: Porcelain disease (caused by the native microsporidia *Thelohania contejeani*),	Infection decreases resource intake in infected native crayfish Invasive crayfish are uninfected	Reduced resource intake of native crayfish reduces both its impact on its invertebrate prey, and its ability to compete thereby potentially facilitating invasion of the larger invasive signal crayfish (*Pacifastacus leniusculus*)	Haddaway et al. 2011.
H: Invasive intertidal snail *Littorina littorea* P: Introduced trematode *Cryptocotyle lingua*	Trematode reduces feeding rates by 40%	In New England, where the snail is the dominant intertidal herbivore, macroalgal cover was found to be 65% higher in experimental enclosures with infected snails than in enclosures with uninfected snails.	Wood et al. 2007.
Parasites of the resource and consumer			

H: Invasive brine shrimp, *Artemia franciscana* P: Native cestodes parasites	Parasites cause reversed phototaxis and colour change in native brine shrimps, but not in the invader	Increased predation rates by definitive hosts (birds) in colour changed shrimps (native) compared to invasive. Parasite modifies predation and inter-specific competition, potentially contributing to invasion success	Georgiev et al. 2007
H: Native amphipod, *Gammarus pulex* and invasive amphipod, *G. roeseli* P: acanthocephalan parasite *Pomphorhynchus laevis*	Parasite manipulates the behaviour of the native amphipod, but not the invader	The native acanthocephalan parasite increases the vulnerability of the native amphipod host to fish predation	Tain, Perrot-Minnot & Cezilly 2007
H: Native *Gammarus duebeni celticus* and three invasive amphipods. P: Native microsporidian, *Pleistophora mulleri*	Infection by *P. mulleri* in native amphipods causes muscle damage and reduced motility. Invasive amphipods are not infected.	Intraguild predation occurs - *P. mulleri* infected individuals showed a reduced ability to predate the smaller invading species and were more vulnerable to predation by the dominant invader *G. pulex*	MacNeil et al. 2003a

H: Native *Gammarus duebeni celticus* and three invasive amphipods. P: Native acanthocephalan *Echinorhynchus truttae*	Infection of the invader reduces its intraguild predation on the native.	Parasitized *G. pulex* showed reduced intraguild predation of the native *G. duebeni celticus* which may slow the displacement of the native species	MacNeil et al. 2003b
Host-mediated parasite-parasite interactions			
H: Humans and wildlife hosts P: TB, malaria and *Toxoplasma gondii*	Infection of T-cells and macrophages by HIV directly impairs host immunocompetence	TB, malaria and *Toxoplasma gondii* increase virulence when coinfections are present	Ezenwa et al. 2010
H: Invasive cabbage moth, *Mamestra brassicae* *P: Baculovirus*	The cabbage moth harbours a persistent asymptomatic infection of baculovirus that is only triggered into a lethal overt state by coinfection with a second, different species of baculovirus.	Coinfection synergises to cause increased host mortality	Burden et al. 2003

H: Humans P: Severe Acute Respiratory Syndrome (SARS) and unidentified respiratory infections	SARS causes respiratory illness and occasional mortality	Coinfection with underlying non-lethal respiratory coinfections created SARS "super-spreaders"	Bassetti et al. 2005
H: Herbivores *Diabrotica virgifera*, and *Spodoptera littoralis* P: Parasitoid *Cotesia marginiventris* and the nematode *Heterorhabditis megidis*	Foliar herbivore *S. littoralis* attacked by parasitoid *C. marginiventris*; root herbivore *D. virgifera* attacked by nematode *H. megidis*; singly infected plants release volatiles that strongly attract the appropriate parasite	Co-infestation with insect herbivores *D. virgifera* and *S. littoralis* reduces production of volatile organic compounds by maize, *Zea mays*, thus reducing attraction of specialist parasites of the insect herbivores,	Rasmann & Turlings 2007
H: Tomatoes *Solanum lycopersicum* P: Parasitic plant dodder (*Cuscuta pentagona*)	Infected tomatoes are less resistant to invasive beet armyworm attack;	Dodder-infected plants are of lower nutritional quality, resulting in reduced growth rates for armyworm caterpillars on coinfected plants	Runyon, Mescher & de Moraes 2008