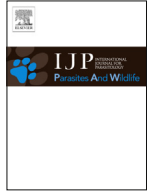




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## Invited Review

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



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## 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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### 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).

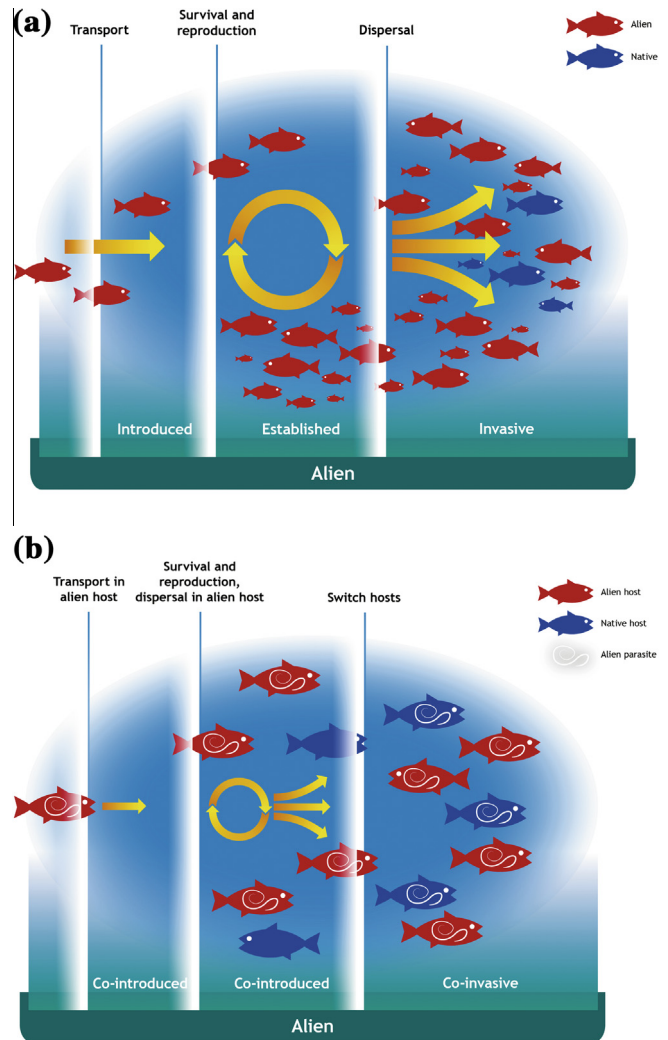
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There has been a dramatic growth in the study of biological invasions in the last twenty years, with a concomitant and confusing amplification of terminology (Falk-Petersen et al., 2006; Blackburn et al., 2011). Blackburn et al. (2011) proposed a unified 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

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